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TEMPORAL AND SPATIAL DISTRIBUTION OF HIGHWAY MORTALITY OF MULE DEER ON NEWLY CONSTRUCTED ROADS AT JORDANELLE RESERVOIR, UTAH

Laura A. Romin[1] and John A. Bissonette[2]

ABSTRACT.—In this paper we evaluated traffic characteristics and vegetative and topographic features associated with mule deer kills on 3 highways (US 40, SR 32, SR 248) in northeastern Utah. We also compared number, and sex and age composition of roadkills to that of the living population observed during spotlight counts. From 15 October 1991 to 14 October 1993 we documented 397 deer roadkills: 51.6% were does, 18.9% bucks, 21.7% fawns, and 7.8% could not be classified. Sixty-seven percent of adult kills were ≤2.5 yr of age. Kill composition compared closely to spotlight counts. Of 1515 spotlighted deer, 65.2% were does, 8.9% bucks, and 25.9% fawns. Spotlight density and deer mortality were strongly correlated from summer 1992 through summer 1993 ($r = 0.94$).

Traffic conditions, topographic features, and vegetative characteristics contributed to mortality levels. Roadkills were highest along US 40 (68% year 1, 55% year 2) where traffic volume and speed were significantly higher than along either state route. Large drainages intersected highways in 78% of designated kill zones. Roads adjacent to agricultural areas along all routes sustained the fewest highway mortalities. Percent cover was higher (40%) in kill zones than in other areas (29%).

Key words: deer, habitat, highway mortality, Odocoileus hemionus, *roadkill.*

In Utah a mean 3115 mule deer (*Odocoileus hemionus*) were killed annually by vehicles during the period 1981–1991 (Utah Division Wildlife Resources 1992). At least 538,000 deer-vehicle collisions occurred nationwide in 1991 (Romin and Bissonette in press). Annual economic loss amounted to $7.8 million, based on average values for each deer killed and vehicle damaged.

Many techniques (e.g., fencing with overpasses and underpasses, swareflex warning reflectors, and highway lighting) have been evaluated in an effort to reduce deer-highway mortality; however, none have provided an effective, cost-efficient solution for widespread use (Reed 1993, Romin and Bissonette in press). Development of successful mitigative technologies relies on an understanding of deer movements onto or across highways.

Topographic and vegetative features, road characteristics, and deer behavior may contribute to deer movement patterns with respect to roads. Published research pertaining to highway mortality of deer has been focused largely on white-tailed deer populations in mixed-hardwood habitat types of Pennsylvania (Peek and Bellis 1969, Vaughan 1970, Bellis and Graves 1971, Puglisi et al. 1974, Carbaugh et al. 1975, Kress 1980, Bashore et al. 1985) and Michigan (Reilly and Green 1974, Allen and McCullough 1976, Kasul 1976, Sicuranza 1979). In general, high concentrations of kill occurred in nonwooded areas and were related to deer foraging pattterns. The juxtaposition of crops and fields to wooded areas influenced deer roadkill locations but varied between studies. In Pennsylvania 58% of white-tailed deer–vehicle accidents occurred in areas where both sides of the road were bordered by fields (Puglisi et al. 1974). In southern Michigan higher accident rates occurred where old fields bordered woods or crops than where cover type was continuous (Sicuranza 1979). Accident locations were not consistent between years (Puglisi et al. 1974). At the roadside, right-of-way topography and vegetation attracted deer, particularly in wooded areas (Carbaugh et al. 1975), and affected deer movements, channeling deer parallel to the road as they foraged (Bellis and Graves 1971).

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Limited studies of mule deer–highway relationships indicated that deer moved along drainages and riparian areas when approaching a road. These routes corresponded with migratory routes of deer (Mansfield and Miller 1975, Reeve 1988).

Highway mortality of both white-tailed and mule deer generally peaked during fall in conjunction with breeding and hunting seasons, with a 2nd, smaller peak occurring in spring, when deer foraged along right-of-ways during greenup (Bellis and Graves 1971, Reilly and Green 1974, Goodwin and Ward 1976, Sicuranza 1979, Dusek et al. 1989). Different patterns of highway mortality are due, in part, to differences in seasonal distribution and migratory patterns of deer (Mansfield and Miller 1975). In studies conducted on deer winter concentration areas in Colorado, virtually all mortality was observed during early spring (Myers 1969).

Relatively few studies compared sex composition of roadkills with that of the living population; yet such comparisons may reveal behavioral traits influencing location and timing of roadkills. The sex ratio of observed roadkills along I-80 in Wyoming was similar to the reported herd composition of 23 male:100 female (Goodwin and Ward 1976). The sex ratio of road-killed adult deer in Wisconsin (Jahn 1959) was not representative of the living population. During fall a higher proportion of bucks were involved in deer-vehicle accidents although the living population showed a higher proportion of does. Similarly, from December through May, yearling males in the Yellowstone area were involved in vehicle accidents in greater proportion than their abundance in the living population (Dusek et al. 1989). Many calculations of live herd composition and number have been based on few spotlight censuses, and reported results may not adequately reflect live population characteristics. Behavioral and habitat use patterns differ among and within species (Kramer 1971, 1973, Geist 1981), and implementation and success of mitigation strategies intended to reduce deer roadkill may be site- or species-specific.

We designed this study (1) to determine whether mule deer roadkills on newly relocated highways would increase and (2) to evaluate the influence of topographic features and vegetation characteristics on the kill pattern. We documented roadkill locations and assessed traffic speed and volume, road alignment, and vegetative and topographic features at areas of high and low kill. We compared live deer-use patterns and roadkill locations to determine the influence of roadside features to deer-vehicle accident locations. Deer–highway mortality levels and composition were compared to that of the living population over a 2-yr period with an extensive data collection study using weekly roadkill collections and repetitive spotlight censuses.

Information obtained through this research effort complements existing research and furthers our understanding of deer-highway relationships. There is limited information that broadly characterizes mule deer use and kill distributions on and near highway systems, or that has investigated the influence of physical landscape features.

STUDY AREA

The study area is located in the valley between the Wasatch and Uintah mountain ranges of northeastern Utah; the Provo River originates in the Uintah mountains and bisects the valley floor. Segments of three highways—

US 40, state routes (SR) 32 and 248, totaling 47.3 km on the eastern slope of the Wasatch mountains in northeastern Utah—were chosen for study. Construction of the roadways was completed in 1989 and was necessitated by inundation of existing roads following construction of Jordanelle Reservoir. Filling commenced in spring 1993.

Dominant valley habitats consist of mesic meadow, riparian areas, and pasture lands. Surrounding drainage slopes are predominantly within a mountain brush and sagebrush-grass zone (6000-7000 ft elevation), with scattered pinyon pine and juniper. Limited stands of aspen, cottonwood, and willow occur. Mule deer utilize the area as year-long range but usually are forced into the valley bottom during winters with heavy snowfall.

METHODS

Deer roadkill data were collected at least once per week by research personnel from 15 October 1991 to 14 October 1993. UDOT and UDWR personnel assisted with collection efforts during their daily activities. Date, highway identification, and location of each kill were recorded to the nearest 0.10 mile. Deer initially were classified as adult or fawn; incisors were removed from adult deer for age determination by cementum annuli procedures (Low and Cowan 1963).

Deer kill zones and nonkill zones were designated based on 1991-1993 deer–highway mortality locations. A minimum of 5 kills per mile had to have occurred for a segment of roadway to be considered a kill zone. A kill zone ended when a section of road did not contain a kill for more than 0.10 mile. We randomly selected 4 kill zone and 4 nonkill zone paired locations of 0.10-mile length along each highway and established transects to evaluate respective road alignment and associated habitat features.

We recorded the distribution of kills over the entire study area, average traffic volume and speed for each highway, percent vegetative cover, and topography proximal to area roads. Kills were recorded to the nearest 0.01 mile. Twice monthly spotlight counts were conducted to document deer use and density adjacent to study area roads. Counts were initiated at dark; each count averaged 3.2 h (s = 21 min). We began the spotlight run on a different route each night. We drove along both sides of each road at a speed of 45–50 kph and used a handheld 400,000 candlepower spotlight to locate deer. Deer were located to the nearest 0.10 mile. We stopped when deer were spotted to identify sex and age class, distinguishing fawns by size. The activity of deer spotted in the right-of-way was classed as feeding, bedding, walking, or standing. We used statistical correlations to compare deer roadkill locations between years and with locations of live deer.

Rangefinder readings were recorded at each 0.1-mile interval to provide an estimate of observable area along each road (Fafarman and DeYoung 1986). Mountainbrush habitats decreased deer visibility, and some areas along roads were not visible from a vehicle due to roadside rock cuts or steep declines bordered by concrete barriers. From numerous spotlight runs, we calculated the mean maximum visible distance to be 500 m.

Deer snow track counts were recorded along the right-of-way once each during the winters 1991–92 and 1992–93 to evaluate deer approaches to the roads. We counted the number of trails within each 0.10-mile interval and described them as either parallel or perpendicular to the road. A parallel trail continued its direction for at least 30 m.

Road alignment, right-of-way width and slope, right-of-way vegetation, and vegetation composition were characterized to a perpendicular distance 100 m beyond the right-of-way fence. Each highway was classified as either 4-lane or 2-lane with passing lanes. UDOT recorded traffic speed and volumes for each road during 2 periods: 11 March to 15 March 1992 and 29 June to 5 July 1992. Road alignments at each selected kill and nonkill transect location were described as curve, hill, or straight section. A curve or hill was considered part of the road alignment if it was within 100 m of the transect. Deer further than 100 m from the road are unlikely to be involved in an immediate collision (Romin and Dalton 1992); thus, beyond this distance, a hill or curve that would have reduced driver visibility had less significance.

We analyzed habitat features during September 1993. Stereoscopic aerial photography (1:24,000) was used to describe habitat features. We placed a transparent grid over photographs to determine percent cover (mountain brush

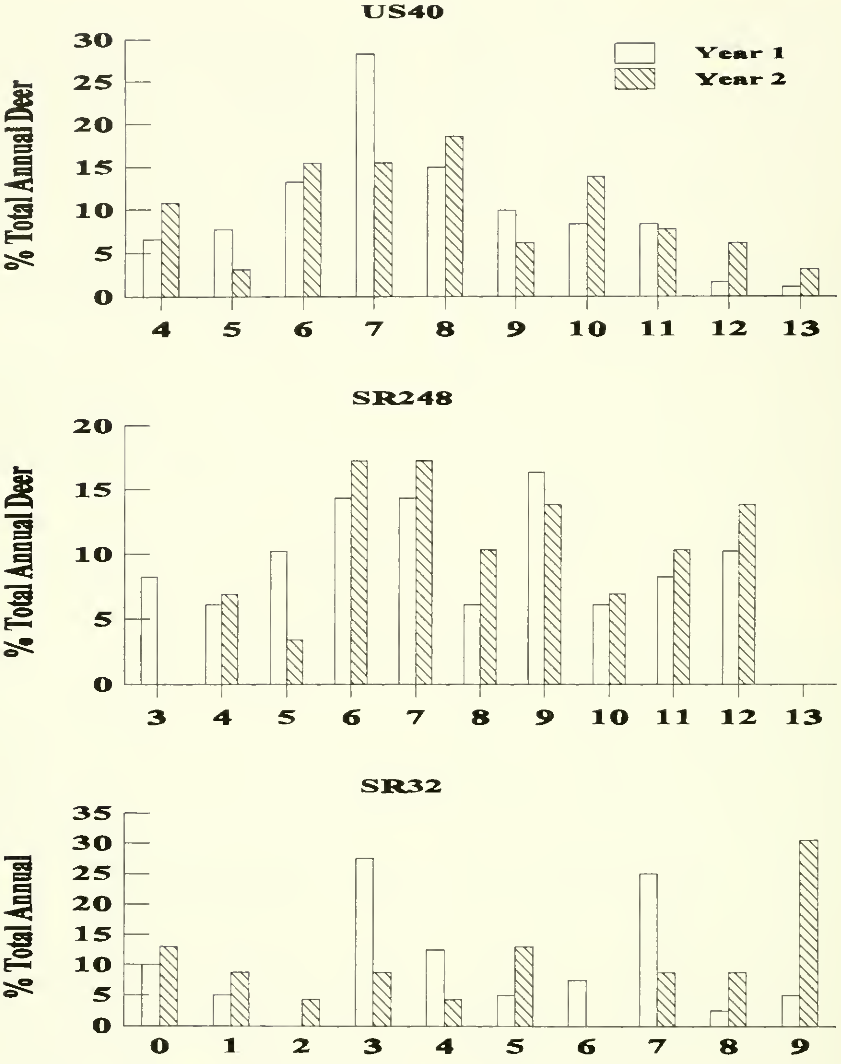

Fig. 1. Distribution of deer kill (%) by mile marker on 3 newly built highways (US 40, SR 248, SR 32) at Jordanelle Reservoir, Utah, 1991–1993.

and riparian areas) and topographical features at deer–highway mortality locations beginning at the road and extending 1.2 km distant. At each paired kill and nonkill location we established 3 habitat transect lines aligned perpendicular to the road. The transects were spaced 100 m apart and extended through the right-of-way zone 100 m past the right-of-way fence. We measured the length of each habitat along each transect line. Habitats included right-of-way revegetation, mountain brush, sagebrush-grass, grass-forb, aspen, cottonwood, willow, agricultural pastureland, riparian, and river. We calculated the proportion of each habitat present along the combined transect lines for each kill and nonkill location.

We identified roadkill and live deer locations, as well as descriptive roadside features to 0.1 mile, consistent with highway mile marker delineation. We converted to metric units for analysis where appropriate.

RESULTS

Deer locations

We documented 397 deer roadkills during the study from 15 October 1991 to 14 October 1993; 278 (5.9 kills/km) kills occurred during

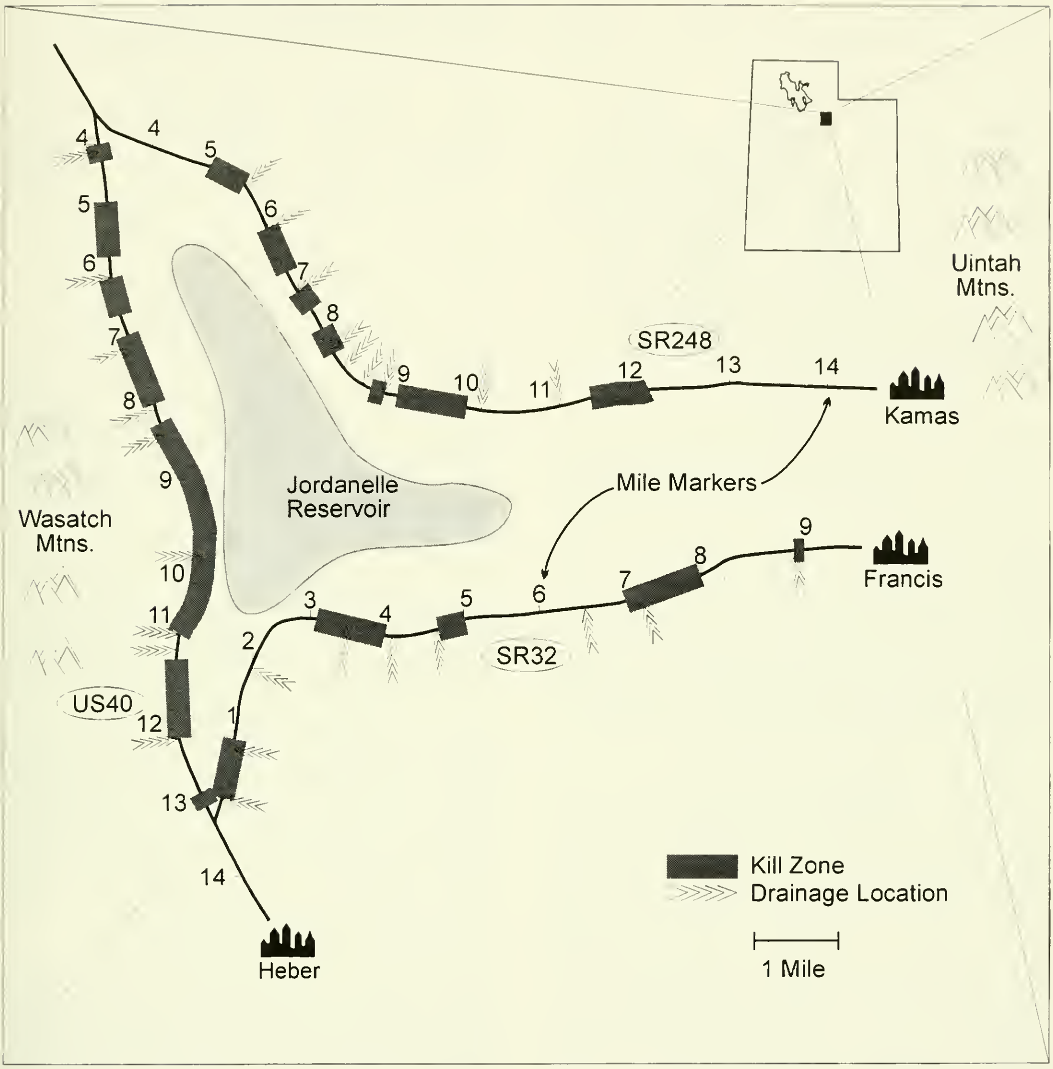

Fig. 2. Location of kill zones and associated drainages at Jordanelle Reservoir, Utah, 1991–1993.

the 1st year of study (15 October 1991 to 14 October 1992), and 119 (2.5 kills/km) were documented during the 2nd year (15 October 1992 to 14 October 1993). Highway US 40 sustained the highest kill levels: 68% during the 1st year and 55% during the 2nd year. State routes 248 and 32 sustained similar kill levels; during the 1st year we recorded 18% and 14% of the total deer-highway mortality on SR 248 and SR 32, respectively. During the 2nd year we recorded 25% of the total annual kill on SR 248 and 19% on SR 32. Deer kills averaged <20 before the roads were relocated.

Nineteen deer kill zones were identified based on the spatial distribution of deer roadkills during both years (Figs. 1, 2). The mean length of kill zones was 1.0 km ($s = 0.62$). Deer-vehicle collisions along US 40 occurred most frequently between mile markers 6.0 and 9.0 during both the 1st (56%) and 2nd (48%) years of the study. Twenty-eight percent of deer roadkills along US 40 occurred from mile marker 7.0 to 7.9 during the 1st year. Roadkill locations were correlated between years along US 40 at both the 1.0-mile ($r = 0.69$, $P = 0.03$) and 0.10-mile ($r = 0.56$, $P < 0.001$) interval. Deer kill locations were not significantly correlated between 1st and 2nd years along SR 32 at either the 1.0-mile ($r = -0.14$, $P = 0.70$) or 0.10-mile ($r = 0.004$, $P = 0.968$)

scale. Deer kill locations along SR 248 were significantly correlated at the 1.0-mile interval ($r = 0.72$, $P = 0.02$) but not at the 0.10-mile interval ($r = 0.18$, $P = 0.07$).

Deer spotlight counts were not significantly correlated to kill locations at the 1.0-mile interval for any road during either year: SR 248 year 1 ($r = 0.43$, $P = 0.19$), year 2 ($r = 0.17$, $P = 0.61$); SR 32 year 1 ($r = 0.42$, $P = 0.23$), year 2 ($r = 0.12$, $P = 0.73$); US 40 year 1 ($r = 0.51$, $P = 0.14$), year 2 ($r = 0.15$, $P = 0.68$). However, positive correlations were stronger during the first year.

Forty percent of spotlighted deer were seen on the right-of-way. We identified the behavior of 968 (55%) of the deer along the right-of-way. Thirty-three percent were standing when first observed, 32% were feeding, 12% were bedded, and 23% were walking along the right-of-way or crossing the road.

Perpendicular snow tracks were not correlated with deer–highway mortality locations ($r = 0.29$, $P = 0.42$). Parallel tracks constituted 48% and 32% of all deer trails counted during the 1st and 2nd years, respectively.

Traffic Characteristics

Traffic characteristics contributed to deer–highway mortality levels (Table 1). Highway US 40 had the highest (3.7–9.9 times) mean 24-hr traffic totals of the 3 study area roads. Mean traffic speed was highest along US 40 (69.3 mph) from 11 March to 15 March 1992; however, over the 4 July weekend (29 June–5 July 1992), average speed along SR 248 (59.1 mph) was slightly higher than along US 40 (58.9 mph). Volume and speed were somewhat higher along SR 248 than along SR 32 for both test dates.

Highway US 40 is a 4-lane road and SR 248 and SR 32 are 2-lane roads with occasional passing zones. Road alignment (Table 2) was similar for transect kill and nonkill zone locations ($\chi^2 = 1.2$, df = 2, $P = 0.70$).

Habitat

From aerial photographs (1:24,000) we determined that percent cover was greater along US 40 (63%) than along SR 248 (28%) or SR 32 (31%). Designated kill zones had higher mean percent cover (40%) than nonkill zones (29%). Highway deer kill along US 40 was highest in an area (mile markers 6.0–9.0) of 88% vegetative cover during both the 1st (56%) and 2nd (48%) years of study. Low mortality occurred in predominantly sagebrush-grass/wet meadow (mile markers 4.0–5.0) or agricultural zones (mile markers 12.3–12.9) with <20% cover. Along SR 248, agricultural zones sustained 1 deer (1%) mortality during the 2-yr period. State route 32 sustained 28% of its total deer road-kill in agricultural areas. However, 50% of this kill occurred at mile marker 9.0, located in a riparian area at an agricultural pasture and cliff interface. During spotlight censuses we observed a larger proportion of deer along right-of-ways associated with mountain brush habitat than along agricultural areas (Table 3). Paired t tests of microhabitat features showed no significant difference in proportion of cover 100 m beyond the fence between kill and nonkill locations ($t = 0.13$, df = 13, $P = 0.90$). Proportion of cover on the right-of-way never was higher than 29% for any transect.

TABLE 1. Traffic speed and volume of new routes at Jordanelle Reservoir, Utah, 1992.

		Speed (mph)		
Date	Location	Mean	Maximum	Vehicles/hr
11 March–15 March	US 40	69.3	76.0	172.2
	SR 248	56.9	72.0	37.9
	SR 32	54.0	68.0	17.3
29 June–5 July	US 40	58.9	68.0	264.6
	SR 248	59.1	63.8	71.4
	SR 32	55.0	68.0	37.8

We examined 19 kill zones and 19 nonkill zones in the study area for associations with drainages (Fig. 2). Since deer-vehicle collisions occurred along nearly all of US 40, we evaluated the 8 highest kill locations along this road. Major drainages intersected the roads in 16 (79%) kill zones. Along US 40, large drainages intersected the highway at 6 (75%) of the kill locations. Two kill zone locations along US 40 were at highway overpasses (mile markers 4.0 and 8.0); drainages were located within 0.2 miles. Two other kill zones extended past highway underpasses (mile markers 8.2 and 11.4) Seven (37%) nonkill zones had drainages intersecting the roads. However, in 4 of the nonkill zones, drainages were within 0.2 miles of a kill zone.

Kill and nonkill locations did not differ in right-of-way widths ($t = 1.1$, df = 13, $P = 0.30$). Deer kill per km was greatest when right-of-way areas were inclined rather than declined or level (Table 4).

TABLE 2. Road alignment at paired ($n = 42$) kill and nonkill locations along study areas routes at Jordanelle Reservoir, Utah.

	Curve	Straight	Hill
Kill	15	23	4
Nonkill	19	21	2

$x^2 = 1.2$, df = 2, $P = 0.70$.

TABLE 3. Deer observed (% of total deer) along right-of-ways associated with agricultural or mountain brush habitat types.

Habitat	US 40	SR 248	SR 32
Agricultural	22	19	23
Mountain brush	49	40	44

TABLE 4. Deer kill per km relative to right-of-way slope relief along both sides of study area roads at Jordanelle Reservoir, Utah, 1991–1993.

	Road		
Right-of-way	US 40	SR 248	SR 32
No incline	6.7	0.9	2.6
Incline 1 side	22.3	6.8	7.1
Incline 2 sides	17.1	9.3	10.6

Temporal Deer Roadkill Distributions

During winter 1991–92, mean monthly snowfall totaled 7.7 cm; mean monthly winter snowfall for 1992–93 was 46.9 cm. Of 397 deer mortalities documented during the study from 15 October 1991 to 14 October 1993, we classified 205 (51.6%) does, 75 (18.9%) bucks, 86 (21.7%) fawns, and 31 (7.8%) unknown. Sixty-four fawns (16.1%) were female and 22 (5.5%) were male (Fig. 3). There was a 57% decrease from 278 (5.9 deer/km) deer roadkills during the 1st year to 119 (2.5 deer/km) roadkills during the 2nd year. We determined the age of 198 (70.7%) adult deer by cementum annuli techniques. Sixty-seven percent ($n = 133$) adult kills were ≤ 2.5 yr old. The oldest recorded deer roadkills (2.5%) were 6.5 yr old. The 1992 hunter buck harvest from the Kamas district, east of the study area, also indicated a young population ($n = 85$); 55% yearlings, 15% 2.5 yr old, and 30% ≥ 3.5 yr old (M. Welch, UDWR, personal communication).

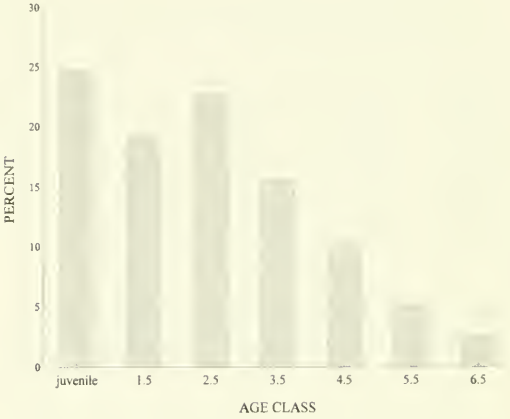

Fig. 3. Deer–highway mortality ages classes ($n = 198$), Jordanelle Reservoir, Utah, 1991–1993.

We located 4378 deer on 39 spotlight trips driving a total of 1845 km. There was a 64.2% decrease from an average 14.6 deer/km^2 in the 1st year of the study to 5.23 deer/km^2 during the 2nd year. UDWR estimated a similar 70% reduction in the deer population on the Kamas District, attributed to the harsh 1992–93 winter (M. Welch, UDWR, personal communication). We identified sex and age of 1515 (34.6%) spotlighted deer: 987 (65.2%) does, 136 (8.9%) bucks, and 392 (25.9%) fawns. We calculated an observable area unobstructed by roadside barriers or dense vegetation of 10.98 km^2 for the study area.

We identified monthly and seasonal peaks in deer mortality (Table 5) by phenological period: fall (September–November), winter (December–February), spring (March–May), and summer (June–August). The following analyses treat the study period as year 1 (15 October 1991–30 August 1992) and year 2 (1 September 1992–14 October 1993), to allow interpretation of seasonal deer distributions and roadkill patterns. The highest roadkill peak (25%) occurred during November 1991. Thirty percent of the mortality in year 1 occurred during the fall even though data collection did not begin until 15 October 1991. Another peak (33%) was evident during the summer of year 1; 15% of the mortality for the year occurred in July. A similar fall peak (52%) occurred during year 2; 20% of the mortality occurred in October and 19% in November. A relatively large peak (18%) occurred in April. Eleven percent of the mortality occurred during the summer. During year 1, 41.8% of the annual

TABLE 5. Seasonal roadkill distributions (%) for each deer class at Jordanelle Reservoir, Utah, October 1991–August 1993.

YEAR 1	Fall	Winter	Spring	Summer
Doe	30.0	16.0	10.2	44.0
Buck	14.5	27.3	16.4	41.8
♀ fawn	57.4	28.6	11.4	2.9
♂ fawn	47.0	40.0	13.0	0.0
YEAR 2				
Doe	65.4	6.2	13.6	14.8
Buck	52.6	10.5	26.3	10.5
♀ fawn	50.0	21.4	28.6	0.0
♂ fawn	40.0	40.0	0.0	20.0

buck mortality and 44.8% of doe mortality occurred during summer (Table 5). Fawn mortality peaked for both males (47%) and females (57.4%) in the fall. During year 2, the highest mortality among all sex and age classes occurred during fall.

Seasonal distributions of deer-highway mortality were compared to observed deer densities during the same periods. Seasonal deer densities and highway mortalities were not significantly correlated ($r = 0.54$, $P = 0.14$) over the 2-year period (Fig. 4). For the period of summer 1992 to summer 1993, deer-highway mortality and deer population density were strongly correlated ($r = 0.94$, $P < 0.01$), suggesting a density-dependent relationship. A negative correlation existed between deer densities and kill/density ($r = -0.68$, $P = 0.06$). During year 1, observed deer density was low during fall (5.4 deer/km^2) and winter (9.9 deer/km^2) while highway mortality was high (fall = 71 deer, winter = 58 deer). Deer density (2.41 deer/ km^2) and highway mortality (18 deer) were low during the 2nd winter. Following winter 1992–93 deer density adjacent to study area roads increased slightly during spring (3.3 deer/km^2) and summer (3.8 deer/km^2). Observed density never reached pre-winter levels. Highway mortality levels of deer also increased ($n = 31$) in spring 1993 but did not return to pre-winter levels. Kill as a function of density was lower than observed deer density from winter 1992 to winter 1993 but exceeded density following the harsh winter of 1992–93 (Fig. 4).

The roadkill buck:doe ratio during fall (22.9:100) and early winter (78.9:100) of year 1 was greater than that observed in the living population (fall = 6.7:100, winter = 4.4:100) during the same periods (Table 6). Likewise,

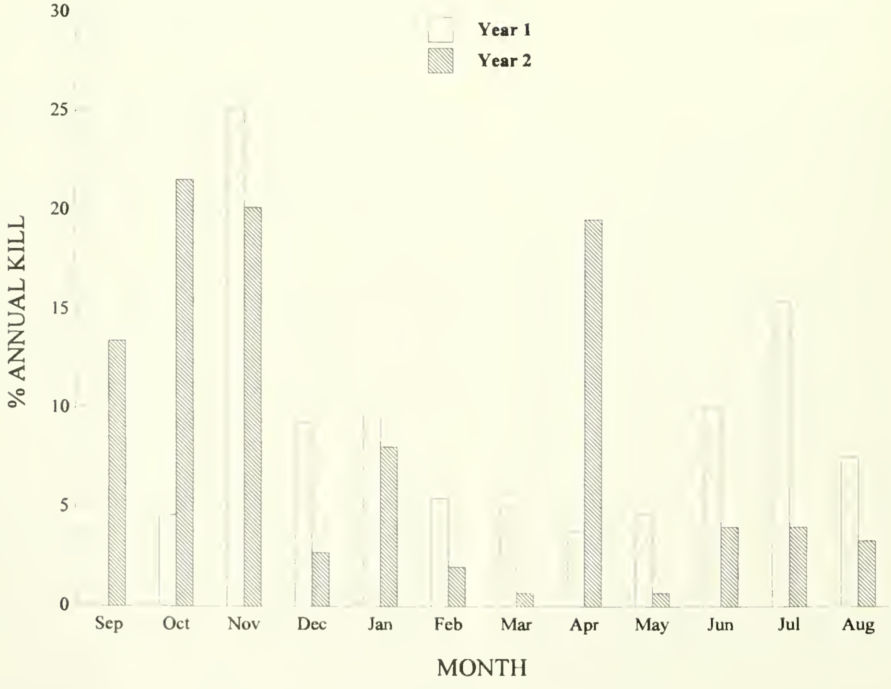

Fig. 4. Monthly deer-highway mortality at Jordanelle Reservoir, Utah, 1991–1993.

TABLE 6. Seasonal buck:doe ratios of roadkill and spotlight deer at Jordanelle Reservoir, Utah, October 1991–October 1993.

	Seasons[b]							
Counts[a]	F91	W91	Sp92	Su92	F92	W92	Sp93	Su93
Kill	22.9	78.9	75	44.2	18.9	40.0	45	16.7
Spotlight	6.7	4.4	2.9	31.3	5.6	0.0	13.3	12.5

[a] Kill and spotlight counts are recorded as bucks:100 does.

[b] Winter counts include only December and early January; spring counts include only April and May. Bucks are probably underrepresented.

the roadkill buck:doe ratio during the fall of year 2 (18.9:100) was larger than the ratio of the living population (5.6:100). The summer buck:doe ratio was similar for roadkill and living populations during both years. For the months June–November 1992, the correlation coefficient between number of fawns involved in vehicular collisions and number observed on spotlight runs was significant: $r = 0.84$ ($P = 0.04$). For both summers the fawn:doe ratio of road-killed animals was 8.3:100, higher than the observed fawn:doe ratio (1.4:100) of the living population.

DISCUSSION

We distinguished aspects of deer mortality based on traffic volume, habitat, topography, and seasonal distribution. Traffic volume significantly influenced overall deer mortality levels. Though total kill in the study area decreased by 57% from the 1st to the 2nd year, roadkills remained higher along US 40 than either SR 248 or SR 32. The 4-lane alignment of US 40 contributed to higher deer kills. Traffic volume was higher and deer-vehicle collisions occurred more frequently along SR 248 than along SR 32 during both years.

Vegetative cover along the length of US 40 was greater than along state routes 248 or 32. Likewise, percent cover was higher for designated kill zones compared to nonkill zones. High percent cover appears to attract deer to right-of-ways for foraging. Agricultural areas provide abundant forage away from roadsides and were associated with low deer–vehicle collision levels. Deer usually approached roads along drainages, and higher kill levels occurred near large drainages.

The ability to predict kill locations requires that kill locations remain similar over time. Kill location correlations at the 0.10-mile interval were low for SR 248 and SR 32 between the 2 yr. The kill locations along US 40 were significantly correlated; however, most of US 40 was considered a continuous kill zone, which would lead to a correlation simply by coincidence.

Although drainages provide highway approaches, it is not possible to predict with exactness where deer-car collisions will occur based on habitat (% cover) and topography proximal to the roads. Deer often move parallel along the right-of-way after approaching a road. However, inclined right-of-ways funneled deer along the highway and were associated with higher kills. Low correlations between spotlight and kill locations further suggest that deer did not immediately cross the roads where they entered right-of-way areas. Snow trail counts also indicated parallel movement of deer.

While seasonal deer–highway mortality distributions tracked large fluctuations in population levels, behavior associated with life history activities of deer, e.g. fawning, breeding, and migration, also influenced year-round roadkill levels and composition. During the 2-yr study period, both roadkill and observed deer density levels decreased. When harsh winter conditions (1992–93) reduced population levels, deer-highway mortality was proportionally lower.

Variability in the association between live deer density and roadkill numbers can be attributed in part to deer-use patterns. Between fall and spring of year 1, highway mortality decreased and spotlight counts recorded increased deer density. The mild winter that year allowed deer access to large areas and they maintained residence higher on drainage slopes. Weather conditions did not force deer to remain near area roads, although they frequently approached and crossed roads. We attributed the initial increase in deer density during spring 1992 to the approach and congregation of deer along right-of-ways for foraging.

Fall peaks in deer-highway mortality appeared related to activities associated with

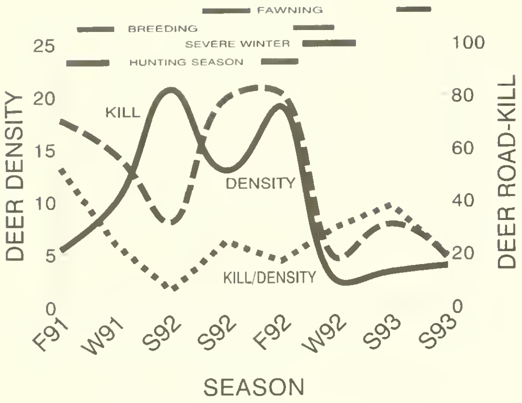

Fig. 5. Seasonal deer-highway mortality (no.) and density (deer/km²) at Jordanelle Reservoir, Utah, 1991–1993.

hunting and breeding during this time (Fig. 5). Deer were moving around the study area more frequently than during other seasons. Proportionally more bucks were involved in vehicular collisions during the fall than were observed in the population. The breeding season of mule deer in Utah begins the last few days of October, peaks between 20 November and 2 December, and declines through January (Robinette and Gashwiler 1950). During the study, Utah deer and elk hunting seasons occurred from late August through October (T. L. Parkin, UDWR, personal communication).

Fawns were involved in deer-vehicle collisions most often during the fall and least often during the summer of both years. The fawning period for mule deer in Utah begins approximately 5 June, reaches and maintains a peak 11–20 June, and declines through 15 August (Robinette and Gashwiler 1950). Fawns are seen infrequently during their first 6–8 wk because their predator defense is based on a "hider" strategy (Geist 1981). Fawns were absent in the observed population during the summer but appeared during the fall.

Does were involved in collisions and observed more frequently than males during both years. Sixty-eight percent of adult deer roadkills were does, while 70% of fawns were female during year 1. Similarly, 81% of adult deer killed were does and 87.5% of fawns were female during year 2. Does have heavy energy demands associated with gestation, parturition, and lactation, which may explain their association with high-quality roadside vegetation and subsequent high mortality rates.

Management Recommendations

Certain topographic features and vegetation characteristics associated with roads, coupled with deer movement dynamics, predispose mule deer to highway mortality. Highway alignment and right-of-way topography often function to funnel deer to the right-of-way and encourage movement of deer along the highway corridor, creating the potential for collisions at numerous locations. Roads planned in high deer-use areas that will sustain high traffic volumes should be prioritized for mitigative procedures during planning. Mitigative technologies, particularly fencing with crossing structures, should focus on the initial approach of deer to the highway along large drainages and take into account deer spatial dynamics and population trends.

Continuing studies designed for species-specific and habitat-specific conditions may further an understanding of why deer-vehicle collisions occur on a spatial and temporal basis, and promote development of appropriate pre-construction designs and mitigation strategies.

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We thank the United States Bureau of Reclamation (BOR), Utah Department of Transportation (UDOT), Utah Division of Wildlife Resources (UDWR), and the United States Fish and Wildlife Service (USFWS) for funding and support provided throughout this study. We extend a special thanks to Larry B. Dalton (UDWR), whose efforts made implementation of this study possible. We sincerely appreciate the efforts of personnel who assisted with roadkill data collection: UDOT (Kamas maintenance shed crew: Shane W. Bushell, Doug C. Gines, Ken L. Moon, Tyler K. Page, and Dave H. Sundquist) and Delmar C. Waters, a private contractor. G. David Cook, Justin L. Dalton, Larry B. Dalton, and Herb C. Freeman provided valuable assistance during spotlight counts.

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EXCEPTIONAL FISH YIELD IN A MID-ELEVATION UTAH TROUT RESERVOIR: EFFECTS OF ANGLING REGULATIONS

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ABSTRACT.—We used creel surveys to evaluate how a change from a 6-mon to a year-round fishing season affected the sport fish harvest in East Canyon Reservoir (Utah), a 277-ha mesoeutrophic system. Under the year-round season, fishing effort was 840 angler-h·ha^{-1}·yr^{-1}, and 360 trout ha^{-1} were captured. Catch rates were proportional to estimated trout densities in the reservoir, ranging from 1.06 during the winter ice fishery, to 0.18 fish angler^{-1}·h^{-1} in July. Ninety-nine percent of fish harvested were rainbow trout (*Oncorhynchus mykiss*). Thirty-two percent of the 300,000 75-mm fingerling trout stocked annually were captured by anglers within 2.5 yr, but return rates varied with the strain and/or size of trout stocked. Annual fish yield was 102 kg/ha, among the highest yet reported for a temperate zone, lacustrine system. Extending fishing from a 6-mon season to year-round increased the number of fish captured and provided almost twice as many hours of recreational fishing in the reservoir. The harvest period was changed from traditional spring–summer months to primarily a winter–spring fishery because relatively few trout survived for more than 6 mon after reaching harvestable size. Although salmonid production in East Canyon Reservoir is very high, the fishery is in a precarious state because high primary productivity driven, in part, by cultural eutrophication, makes water quality suboptimal during midsummer.

Key words: reservoir, yield, trout, creel, harvest, strains, regulation, productivity, fish, management, growth, Oncorhynchus mykiss.

Important goals of lake and reservoir management are to maximize both fish yield and recreational use. Methods of increasing yield include introducing different species or strains, lake fertilization, and modifying fishing regulations (Hall and Van Den Avyle 1986, Stockner 1992). Modification of littoral zone escape habitat may also be important (Wurtsbaugh et al. 1975, Trendall 1988, Tabor and Wurtsbaugh 1991). Changes in fishing regulations, however, offer a manager the most flexibility (Carlton 1975), and these changes are less likely to damage the ecosystem than are the other methods. In 1985 the State of Utah changed from a 6-mon open season for trout (late May–November) with a daily limit of 8 fish, to a year-round fishery with no seasonal closures and a daily limit of 8 fish. To investigate how this management change affected the fishery, we conducted a 1-yr creel survey in 1986 to determine timing and magnitude of harvest from East Canyon Reservoir: we then compared these results with harvest characteristics measured in the reservoir in 1970 and 1972 under the 6-mon regulation. The 1986 creel survey also allowed us to measure the high fish yield of the reservoir and to relate it to various limnological parameters affecting fish production (Carline 1986). We were also able to investigate how different strains of trout stocked in the reservoir recruited to the fishery (Brauhn and Kincaid 1982, Babey and Berry 1989). This work was part of a comprehensive study on the ecology and causes of mortality of stocked rainbow trout in mid-elevation reservoirs in Utah.

STUDY AREA

East Canyon Reservoir is located at an elevation of 1734 m in northern Utah (Morgan County; 40°54′N, 110°35′W). East Canyon Creek and other minor tributaries of the reservoir drain a 99,200-ha watershed in the calcareous Wasatch Mountains. At full pool the reservoir is 5.6 km long, 60 m deep, and covers 277 ha (Table 1). The reservoir is productive, with a mean summer (May–Oct) chlorophyll *a* concentration of 5.4 mg/m^3 (1985–86 and 1989–90 mean), and a mean Secchi depth of 4.6 m (W. Wurtsbaugh unpublished data). Blooms of cyanobacteria occur frequently during summer and fall. Annual total phosphorus (TP) loading of 2.8 g m^{-2}yr^{-1} is very high

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TABLE 1. Limnological characteristics of East Canyon Reservoir, Utah. Data sources: [a]Utah Department of Health (1982); [b]Merritt et al. 1980. Other data are unpublished data of W. Wurtsbaugh.

Elevation[a]	1734 m
Area (full pool)[a]	277 ha
Volume (full pool)[a]	63,200 m^3
Mean and maximum depths[a]	23 & 60 m
Shoreline length[a]	16 km
Chlorophyll *a* (May–Oct)	5.4 $\mu g/L$
Secchi depth (May–Oct)	4.6 m
Alkalinity[a]	3.4 mEquiv
Total hardness[a]	233 mg/L
Total dissolved solids[a]	328 mg/L
Annual phosphorus loading[b]	2.8 $g\ m^{-2} \cdot yr^{-1}$
Mean water column total phosphorus[a]	80 $\mu g/L$

(Merritt et al. 1980), and mean water column TP is 80 $\mu g/L$ (Utah Department of Health 1982). Algal growth in the reservoir, however, is limited primarily by nitrogen (Wurtsbaugh 1988). The reservoir's water level fluctuates widely because of water withdrawals for irrigation, and consequently there is little macrophyte development in the littoral zone. During much of the summer, oxygen concentrations in the hypolimnion drop below 1 mg/L. Epilimnetic temperatures reach 22°C in July, and the reservoir is typically ice covered from late December through March. During much of the year high densities (>10/L) of *Daphnia pulex*, *D. galeata*, and other crustacean zooplankton are evident (Tabor and Wurtsbaugh 1991, W. Wurtsbaugh unpublished data). Additional limnological information is given in Table 1.

Dominant fishes in the lake, in approximate order of biomass, are Utah suckers (*Catostomus ardens*), redside shiners (*Richardsonius balteatus*), and rainbow trout (*Oncorhynchus mykiss*). Less-abundant species are cutthroat trout (*O. clarki*), brown trout (*Salmo trutta*), speckled dace (*Rhinichthys osculus*), fathead minnows (*Pimephales promelas*), and kokanee (*O. nerka*). Rainbow trout are heavily parasitized by anchor worms (*Lernaea cyprinacea*; Berry et al. 1991).

In late May the Utah Division of Wildlife Resources stocks 300,000 (1080/ha) rainbow trout, approximately 75 mm in length, in East Canyon Reservoir. Fish captured by anglers during our 1986 creel survey were derived from several strains of rainbow trout stocked in 1984–1986 (Table 2). Each strain stocked in the reservoir was spray marked with a different color of fluorescent pigment (Phinney et al. 1967, Vondracek et al. 1980).

Trout grow quickly in East Canyon Reservoir and enter the fishery within 5 mon. The reservoir is intensively fished due to its proximity to 2 major population centers, Salt Lake City and Ogden. Creel surveys in the 1970s indicated fishing effort at over 300 angler-$h \cdot ha^{-1} \cdot yr^{-1}$. Because anglers fish primarily with bait, there is little catch-and-release fishing. Most trout captured are less than 350 mm. Schrader (1988), Babey and Berry (1989), and Tabor and Wurtsbaugh (1991) provide additional information on the fish and fishery.

METHODS

Creel data were collected during 1970, 1972, and 1986 by interviewing anglers and by counting the total number of anglers on the reservoir. Sampling effort was stratified by weekday and weekend, month, time of day (morning, midday, and evening), and method of fishing (ice, shore, and boat), with random samples taken within each stratum (Malvestuto 1983). The creel clerk determined the number of fish released and the number, length, and weight (1986 only) of each species or strain kept. In 1986, 25% of the weights were not measured. These were subsequently estimated with an empirically derived length-weight regression for rainbow trout:

$$W = 1.619\ 10^{-5} \cdot TL^{2.949}\ ;\ R^2 = 0.95,$$

where W = wet weight in grams and TL = total length in mm. Sample estimates were expanded to provide monthly and seasonal totals for fish harvests and angler use.

Details of the methods varied somewhat between surveys in the 1970s and those in 1986. In 1986 we sampled 5 weekdays and 4 weekend/holidays each month of the year. In 1970 and 1972 the sampling interval lasted only from opening day (Memorial Day weekend) through August. Creel surveys in 1970 and 1972 were done on both days of the opening weekend: during the remainder of the sampling period the reservoir was randomly censused on 20 (1970) or 48 d (1972). Because catch information was unavailable for the September–November periods in 1970 and 1972, we restricted comparison with the 1986 catch statistics to the January–August interval. Nevertheless, in 1986,

TABLE 2. Sizes (± standard deviation) and percentages of rainbow trout strains planted in East Canyon Reservoir from 1984 to 1986, and percent of those fish captured by anglers during 1986. Each year 300,000 fish were stocked in the reservoir. Relative return of each strain was calculated: [100 (% returned / % stocked)] –100. A large (L) and small (S) group of Ten Sleep strain were planted in 1986. Shepherd = Shepherd of the Hills strain.

Strain–Size	Mean stocked weight (g) ±*s*	% stocked	Number captured	% captured	Relative return
			1984		
Kamloop	4.7 ± 1.4	32	2,300	25	–22
Ten Sleep	5.0 ± 1.6	36	2,400	26	–28
McConaughy	5.8 ± 3.1	32	4,500	49	+53
			1985		
Kamloop	7.5 ± 2.3	33	33,000	43	+30
Ten Sleep	5.4 ± 1.4	33	27,700	36	+9
Shepherd	3.7 ± 1.4	33	16,100	21	–37
			1986		
Ten Sleep–L	4.8 ± 1.4	25	3,300	26	+4
Ten Sleep–S	3.1 ± 1.1	25	2,800	22	–12
Shepherd	4.2 ± 1.4	50	6,700	52	+5

85% of the effort and 81% of the annual rainbow trout harvest occurred by the end of August (see below), indicating that earlier surveys provided a reasonable assessment of the fishery.

During 1986 we identified fluorescent-marked rainbow strains using a portable, battery-powered black light affixed within a light-exclusion box. Fish captured during the year they were planted were designated age 0, and those captured during the 2nd and 3rd year after planting as age 1 and age 2, respectively. We analyzed creel data with the FORTRAN program WCREEL, supplied by the Utah Division of Wildlife Resources (B. Schmidt personal communication).

Temporal changes in trout abundance in a put-grow-and-take fishery such as that in East Canyon Reservoir can be evaluated by the number of fish removed from the system by anglers because relatively little mortality occurs from other factors after trout attain a harvestable size. For example, estimated losses of all sizes of trout to birds, which has been shown to be important in some Utah reservoirs (Wasowicz 1991) and elsewhere (Matkowski 1989), accounts for approximately 6% of planted trout in East Canyon Reservoir (R. A. Tabor unpublished data). Piscivorous fish eat over 25% of stocked trout, but this loss is negligible once prey reach 150 mm (Wurtsbaugh 1987 and unpublished data). Furthermore, because the reservoir has a deep release, located in the hypolimnion, we believe that few fish emigrate, although we lack quantitative data to support this.

Had we used this approach to estimate abundance of trout planted in 1985 that reached harvestable size, we would have required creel data from at least 3 consecutive years (1985–1987), or until anglers had removed all of the cohort. Because we measured harvest only during 1986, and thus lacked a long-term data set, we assumed that harvests of age 0 fish in 1985 and age 2 fish in 1987 were similar to the measured harvest of age 0 (stocked 1986) and age 2 (stocked 1984) fish during 1986. Because 80–90% of each strain was harvested as age-1 fish (see below), violations of this assumption should not have seriously affected our analysis.

To determine the effect of trout density in the reservoir on monthly success rates for anglers, we graphed the estimated density of fish remaining to be captured from the 1985 cohort against catch per hour for fish in that cohort. At the beginning of the survey in January 1986, we estimated that 67,400 fish from the 1985 cohort were available in the reservoir. This density was based on total catch of the cohort in 1986 plus an additional 9000 fish estimated to have survived into 1987. Nine thousand (3%) of the 1984 cohort survived over 1 yr and were captured by anglers in 1986. Fish densities for subsequent months were calculated by subtracting the previous month's harvest. The resulting regression from this analysis may include some bias, since measurements of fish densities each month were not independent of each other. For this reason we did not calculate statistical significance levels for the regression. Nevertheless, the approach yields a useful estimate of the relationship between abundance and catch rates.

To estimate the mortality of trout that were captured and then released by anglers, we assumed a survival rate of 69% (Taylor and White 1992). Because sizes and ages of these released fish were unknown, we assigned proportions to the different year classes. Our interviews with anglers indicated the main reason fish were released was because of small size, but a limited number were also returned because of the presence of ectoparasites (*Lernaea*) or their scars. We therefore assumed that 90% of returned fish were age 0 (i.e., returned because of small size), 10% were age 1 (returned for cosmetic reasons), and no age 2 were returned.

RESULTS

The Fishery Under a Six-month Season

Under the 6-mon open season documented in 1970 and 1972, fishing was concentrated from the opening weekend in late May through August. Fishing on the opening weekend accounted for 16–21% of the estimated total effort, and 28–38% of the rainbow trout harvest (Table 3). Fishing pressure dropped steadily through the summer, and catch rates varied from 0.18 to 0.49 trout/h. Total fishing effort was similar in 1970 and 1972, with the lake providing over 350 angling-h/ha. Anglers harvested an estimated 60,100 rainbow trout during the survey period in 1970, but only 35,600 in 1972 (Table 4). The catch rate for rainbow trout in July 1972 was much lower than in other months. This was due, in part, to anglers fishing for kokanee and a strain of albino rainbow trout that made up 44% of the July harvest. The total catch rate of 0.32 fish/h was comparable to other months of the year when kokanee and albino trout were harvested less (4% of the catch in June and 9% in August).

The Year-round Fishery

Trout grew rapidly in East Canyon Reservoir, particularly during their 1st year (Fig. 1). Fish were planted in May at a mean size of 75 mm and 3.8 g. When they first entered the fishery in July, they were 178 mm and 77 g. By July, the previous year's cohort of fish had reached 305 mm and 420 g. By the end of the 3rd year, fish had reached 400 mm and 728 g.

In 1986 anglers spent over 230,000 h (±9300, $s_{\bar{x}}$) fishing in East Canyon Reservoir, or 840 angler-h·ha^{-1}·yr^{-1}. Most of these hours were by shore anglers (58%), followed by boat

TABLE 3. Pressure, harvest, and catch rates for rainbow trout for creel surveys conducted in 1970, 1972, and 1986 for the January–August period. Earlier surveys lasted only from the opening weekend (Memorial Day—the last weekend in May) through August. In 1986 the state changed to a year-round season, so there was no opening day. Only the January–August data of 1986 are shown here to facilitate comparisons between the 2 periods. Total catch for the year is shown in Table 4.

	Jan–May	Opening weekend	June	July	August	Total Jan–Aug
			1970			
Effort (h)	—	19,100	58,600	28,600	13,600	119,900
Harvest (number)	—	18,300	21,900	13,900	6,000	60,100
Catch rate (fish/h)	—	0.96	0.37	0.49	0.44	0.50
			1972			
Effort (h)	—	22,100	40,700	32,500	11,600	106,900
Harvest (number)	—	13,400	12,600	5,800	3,800	35,600
Catch rate (fish/h)	—	0.61	0.31	0.18	0.33	0.33
			1986			
Effort (h)	118,000	—	42,400	22,700	15,900	199,000
Harvest (number)	66,800	—	8,300	3,200	2,500	80,800
Catch rate (fish/h)	0.57	—	0.20	0.14	0.16	0.41

TABLE 4. Total catch of salmonids from East Canyon Reservoir in 1970, 1972, and 1986. In 1970 and 1972 yields were estimated from the start of the fishing season, in June, through August. Data for 1986 show captures during the entire year. Table 3 shows the comparable catch in 1986 from the opening day through August.

	1970	1972	1986
TAXA			
Rainbow trout	60,100	35,600	98,960
Albino rainbow trout[a]	—	1,200	—
Brown trout	200	20	60
Cutthroat trout	0	500	700
Kokanee[a]	—	3,900	100
TOTAL	60,300	42,220	99,820

[a] First stocked in 1970

(24%) and ice anglers (18%). The relative distribution of angling type varied seasonally: In January and February, nearly all fishing was done through the ice, but subsequent fishing pressure was dominated by boat and particularly shore anglers (Fig. 2A). Total fishing pressure reached a peak during May, the period of the traditional opening day.

Monthly catch rates for rainbow trout varied from a high of 1.06 fish/angler-h in February to 0.18 in July (Fig. 2B). Annual catch rates were 0.92 for ice anglers, 0.34 for boat anglers, and 0.30 fish/h for shore anglers. The average for all types of fishing was 0.42 fish/h. Catch rates for ice anglers in January and February were the highest for any month or method for the year (Fig. 2B).

There was a strong relationship between the estimated density of trout from the 1985 cohort remaining to be captured and monthly catch rates for those fish (Fig. 3). In January and February when there were more than 200 fish/ha (0.2 fish/m^2) in the reservoir, catch rates were over 0.6 fish/angler-h. As densities dropped, however, catch rates declined progressively, reaching a low of 0.1 fish/angler-h in December.

We estimate that 99,300 ± 7500 $(s_{\bar{x}})$ game fish were removed from East Canyon Reservoir by anglers in 1986. Of these, 99.1% were rainbow trout, 0.7% were cutthroat trout, 0.1% were kokanee salmon, and <0.1% were brown trout. Sixty-eight percent of the annual harvest of rainbow trout occurred from January through May, and 38% of these were captured in January and February during the ice-fishing season (Fig. 2C). Rainbow trout planted the previous year (1985) dominated the catch from January to August of 1986 (Fig. 2C). Rainbow trout planted in May 1986 first entered the fishery at a mean total length of only 178 mm in July, and by October this cohort dominated the harvest. Although age 0 and age 2 fish were important in the fishery early and late in the year, 78% of the total catch was of age 1 fish from the 1985 planting.

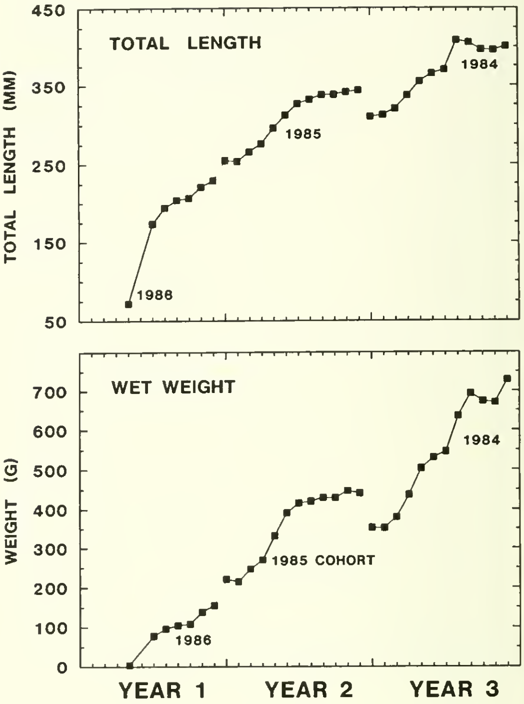

Fig. 1. Changes in total lengths (above) and wet weights (below) of the 1984, 1985, and 1986 cohorts of rainbow trout captured by anglers in East Canyon Reservoir. All fish were captured during 1986 but are plotted over a 2.5-yr period to show long-term growth rates. Also plotted are initial lengths and weights of the fish stocked in 1986. Total lengths (TL) can be converted to standard lengths (SL) by dividing by 1.15.

Anglers released 37,000 hooked fish during 1986, giving an estimated mortality of 10,400 fish during the 1st year they were in the reservoir and an additional 1100 in the 2nd year. Consequently, approximately 4% of stocked fish are lost because of hooking mortality. About 75% of this mortality occurred from July through December when small trout first entered the fishery.

Total fish yield in East Canyon Reservoir during 1986 was 102 kg/ha. Most of the harvest occurred before July (Figs. 2C, 2D). Fish planted the previous year represented 82% of the biomass of rainbow trout captured in 1986.

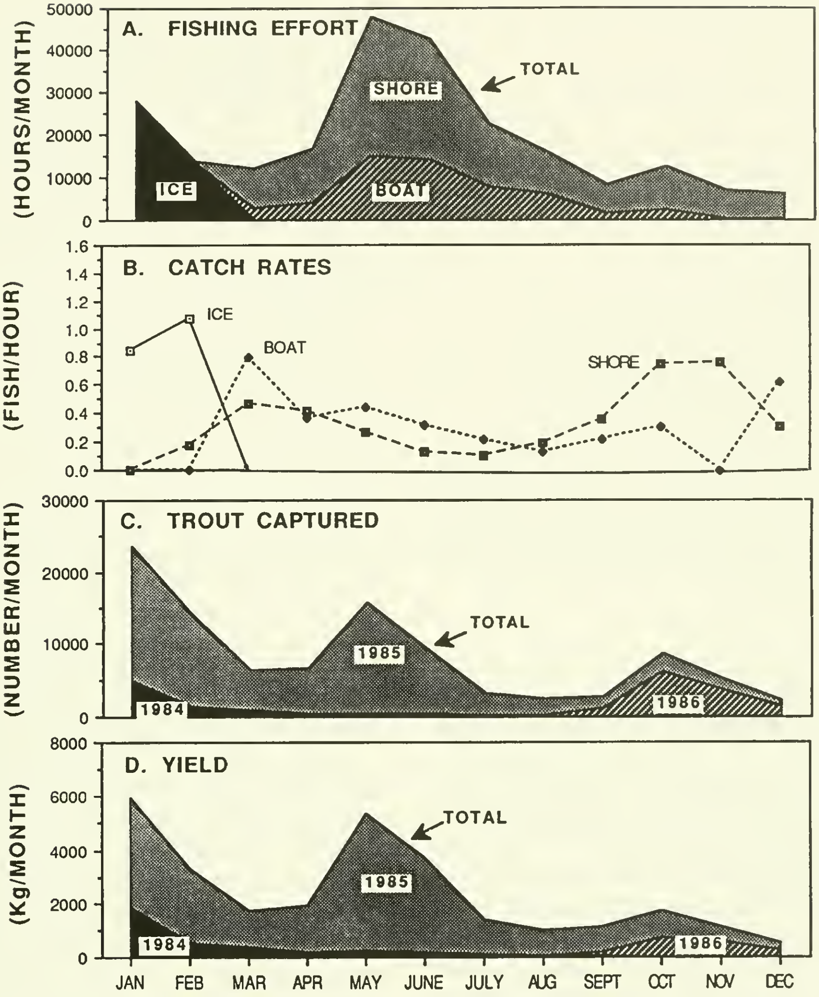

Fig. 2. Seasonal changes in fishing effort and rainbow trout captured during 1986 in East Canyon Reservoir. A, Frequency polygon of seasonal changes in effort expended in ice fishery (ice), boat angling, and shore angling (top line shows total fishing effort); B, monthly changes in catch rates for the 3 fishing methods; C, numbers of rainbow trout captured each month during 1986 from the 1984, 1985, and 1986 cohorts of rainbow trout planted in the reservoir; D, total and component yield of trout from each cohort captured during 1986.

Harvest of Different Strains

Four strains were in the reservoir during 1986 as a result of stocking in 1984, 1985, and 1986 (Table 2). Relative proportions of each strain harvested fluctuated seasonally. McConaughy strain from the 1984 stock and Kamloop trout from 1985 were captured more than expected in the winter and spring catches of 1986. In the summer, however, catch rates of Kamloop and Ten Sleep from the 1985 stocking were similar for the rest of the year. Shepherd of the Hills strain stocked in 1985 was harvested less than the other two strains planted that year. During 1986 there were significant differences in harvest rates of different strains planted in 1984 ($X^2 = 13.34$, $P < 0.05$) and in 1985 ($X^2 = 7.76$, $P < 0.05$), but not in 1986.

A large percentage of each strain stocked in the reservoir was eventually captured by anglers. There were, however, considerable differences in relative return of different strains. We estimate that 40% of Kamloop, 32% of Ten Sleep, and only 23% of Shepherd of the Hills strain were captured during their first 2 1/2 yr in the reservoir (Fig. 4). For all strains combined, 32% of the fish stocked were eventually captured by anglers.

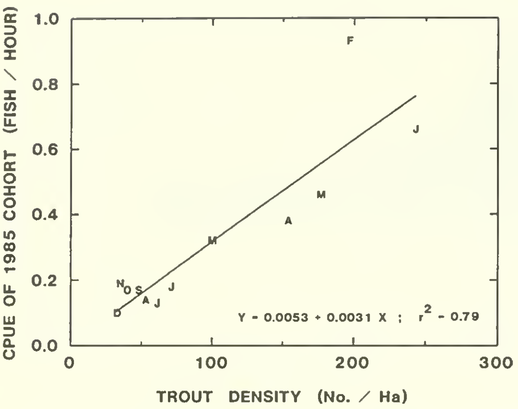

Fig. 3. Relationship between monthly estimates of the density of rainbow trout remaining in the 1985 cohort and catch per unit effort (CPUE) for those fish in the reservoir. The CPUE shown here is less than in Figure 2B because it does not include fish from 1984 and 1986 cohorts that were captured, nor the capture of other species. Letters on graph indicate months.

DISCUSSION

The fishing regulation change in East Canyon Reservoir resulted in an excellent winter ice fishery but poorer summer angling than when a 6-mon season was in effect. In 1970 and 1972 anglers harvested 30–37% of the annual total during the intensive 3-d opening (Table 3), but large numbers of fish still remained in the lake to support a summer fishery with catch rates of 0.3–0.5 fish/h. In 1986, however, about 66% of the fish had been harvested in the winter and spring fishery by the time of the traditional opening day. Monthly estimates of pressure during the summer fishery (June–August) for 1986 were similar to those in the earlier studies (Table 3), but the summer harvest was only 33–64% of that in previous years.

While failing to maintain the traditional catch rate for summer months, the regulation change may have provided a fishery that not only produced increased numbers of fish over a longer period of time, but also provided almost twice as many hours of recreational fishing as under the 6-mon open season (Table 3). If the popularity of winter angling were to increase substantially, an even larger proportion of trout would be captured then, leaving fewer for the traditional spring and summer fisheries. To spread the catch over a longer period, the State of Utah reduced the winter bag limit to 4 fish subsequent to our study. The differences noted under the different angling regulations must be treated cautiously, however, as only 1 yr of data was available for the year-round season, and substantial between-year differences were noted for the 1970 and 1972 period. Factors such as changing predation pressure from piscivores and changes in nutrient loading to the reservoir undoubtedly also contributed to changes in the fishery.

Catch rates for the 1985 cohort of fish were clearly related to monthly changes in the density of these fish (Fig. 3), but there may have been additional factors influencing fishing success. Catch rates in February were higher than the prediction based on density. The reason for this is not clear, but it is possible that catch rates were especially high during midwinter when available food was low. Catch rates in June–August were somewhat below the regression, perhaps because during warm months of the year fish are concentrated in deeper water near the thermocline where they are more difficult for anglers to reach. Catch rates increased, relative to the regression, in the fall (September–November) when the reservoir began to cool. Despite relative minor seasonal shifts, it appears that densities of rainbow trout available in the reservoir can explain most of the variation in catch rates.

Significant differences in the relative harvest of different strains of rainbow trout were not unexpected, as others have found that strains stocked can have large effects on the fishery (e.g., Brauhn and Kincaid 1982, Babey and Berry 1989). The poor return for Shepherd of the Hills strain (Table 2) is consistent with the poor return of this group in East Canyon Reservoir reported by Babey and Berry (1989). Nevertheless, 2 factors confound the interpretation of these results. First, despite efforts to control sizes of fish planted, there were sometimes substantial differences in weights of different strains stocked. For each annual cohort, the relative return of a strain was correlated with its size at stocking (Table 2); groups stocked at a large size usually survived better than smaller ones. Second, because our creel survey lasted only 1 yr, we could not determine if some strains entered the fishery as quickly as others. For example, the very high relative return rate of the McConaughy strain in 1986 may be a consequence of a very low catch rate of these fish measured in 1984 and

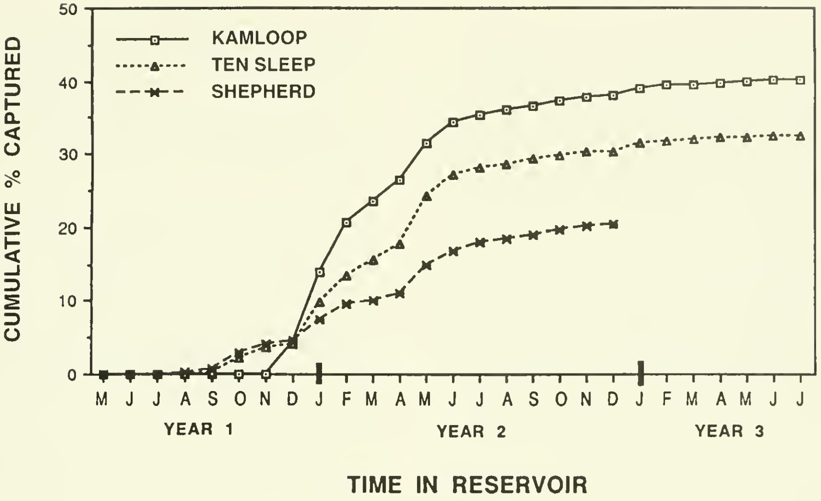

Fig. 4. Cumulative monthly increase in the percent of fish captured from 3 strains of trout stocked in 1985. The creel survey was conducted for only 12 mon, but data were expanded to cover a longer period by using information on other cohorts (see text).

1985 (Schrader 1988). Consequently, in our study and in many others (see Babey and Berry 1989) that have investigated the importance of fish strains, results are confounded because strain size and condition were not carefully controlled, and because the harvest of fishes was not measured over their entire life span.

The fish yield of 102 kg/ha in East Canyon Reservoir is among the highest yet reported for a temperate zone lake (Morgan et al. 1980, Jones and Hoyer 1982, Schlesinger and Regier 1982) and is as high as yields in many tropical systems (Morgan et al. 1980). It is also high in relation to chlorophyll levels in the lake. Regressions with summer chlorophyll levels would predict yields ranging from 4 to 13 kg/ha, depending on the model chosen (Ogelsby 1977, Jones and Hoyer 1982; see Carline 1986). A model based on total phosphorus would predict salmonid *production* of only 22 kg/h (Plante and Downing 1993), so the realized *yield* of 102 kg/ha is far above expectations (Downing and Plante 1993). Even when the weight of fish stocked (5 kg/ha) is subtracted from total yield, harvest from this cold-water reservoir is still remarkably high.

Several characteristics of the reservoir and fishery may contribute to the high yield. First, high nutrient loading (Merritt et al. 1980) produces high algal productivity that in turn supports a large zooplankton population dominated by *Daphnia* (this, however, does not explain why fish production is higher than that predicted by chlorophyll or phosphorus levels). Second, rainbow trout in East Canyon Reservoir are primarily first-order carnivores, feeding throughout most of their lives on large *Daphnia* spp. (Tabor et al. in press). They begin feeding on other fish only when they exceed about 370 mm total length (Wurtsbaugh 1987). Third, the management agency takes full advantage of high productivity by stocking large numbers of fish. Fourth, with intense fishing pressure, most of the trout are harvested thoroughly and quickly while they are growing rapidly (Fig. 1). The combined effects of high reservoir productivity, high stocking density, trout feeding close to the base of the food web, and intensive fishing pressure contribute to the very high fish yield.

Although East Canyon Reservoir has provided exceptional trout yields, there are indications that high nutrient loading from residential and recreational development in the headwaters of the drainage may be pushing the fishery toward collapse. Because the reservoir is already mesoeutrophic, increased productivity resulting from development may further deplete oxygen in the hypolimnion and metalimnion. Oxygen and temperature profiles we took in July and August 1985 and 1986 demonstrated that water with O_2 concentrations >5 μg/L was found only at depths above 10 m where temperatures were above

18° C. Summer metalimnetic and hypolimnetic oxygen concentrations in 1985 and 1986 were much lower than reported for the reservoir during 1978–1980 (Merritt et al. 1980, Utah Department of Health 1982). When oxygen is lost from these layers, fish are forced into the warm epilimnetic water. Because optimal temperatures for rainbow trout are near 15–18° C (Hokanson et al. 1977, Wurtsbaugh and Davis 1977), and because O_2 concentrations for salmonids should be at or above 5 μg/L (Brett 1979, EPA 1986), the situation in East Canyon Reservoir may become too stressful for rainbow trout, and they may be squeezed into a narrow metalimnion where conditions are suboptimal. Indications that trout are stressed include poor growth in midsummer (Fig. 1; Babey and Berry 1989), increases in *Lernaea* infestation from 20/fish in the 1970s to 40/fish in the late 1980s (T. Pettengill unpublished data), and complete failure of the 1989 and 1991 year-classes subsequent to our field study. Loss of salmonid fisheries with increasing eutrophication is common (Colby et al. 1972). Consequently, urban planners and fishery managers should limit reservoir nutrient loading to maintain adequate summer oxygen levels and thus ensure that the outstanding family fishery for salmonids in the reservoir is maintained.

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CONSUMPTION OF DIFFUSE KNAPWEED BY TWO SPECIES OF POLYPHAGOUS GRASSHOPPERS (ORTHOPTERA: ACRIDIDAE) IN SOUTHERN IDAHO

Dennis J. Fielding[1,2], M. A. Brusven[1], and L. P. Kish[1]

ABSTRACT.—Consumption of diffuse knapweed (*Centaurea diffusa* Lam.) by 2 polyphagous grasshopper species, *Melanoplus sanguinipes* (F.) and *Oedaleonotus enigma* (Scudder), was studied using microhistological analysis of grasshopper crop contents. Grasshoppers were confined to cages containing *C. diffusa* and *Sisymbrium altissimum* L., a member of the mustard family known to be readily eaten by these 2 grasshopper species. Preference indices for knapweed were lower than for *S. altissimum* in 4 of 5 trials. An uncaged population of *M. sanguinipes* on a knapweed-infested site consumed only small amounts of knapweed until late summer when most other plants were senescent. Results suggest that diffuse knapweed's low palatability to generalist herbivores may confer to it a competitive advantage over other rangeland plants.

Key words: Centaurea diffusa *Lam., diffuse knapweed, herbivory, insects, competition.*

Diffuse and spotted knapweed, *Centaurea diffusa* Lam. and *C. maculosa* Lam., respectively, were introduced to the Pacific Northwest around 1900 (Watson and Renney 1974). Since then they have rapidly spread throughout the area (Fig. 1; Forcella and Harvey 1981). Heavy infestations of knapweed reduce production of more desirable species of forage plants, thus reducing the value of rangeland for grazing and wildlife habitat. Several specialist insect herbivores have been introduced in attempts to control knapweed (Story and Anderson 1978, Maddox 1979). To date, no studies have reported on the consumption of knapweed by polyphagous insect herbivores.

Cnicin, a sesquiterpene lactone, is produced by spotted and diffuse knapweed (Drodz 1966, Locken and Kelsey 1987). Picman (1986) suggested that sesquiterpene lactones have toxic effects on many herbivores and may function as deterrents to herbivory. Locken and Kelsey (1987) suggested that nonpalatability of knapweeds may afford them a competitive advantage over many other plant species by protecting them from herbivory. Grasshoppers (Orthoptera: Acrididae) are a conspicuous and important class of herbivores on rangeland in the western U.S.

Rangeland grasshopper populations in southern Idaho occasionally reach outbreak proportions. Two species in particular, *Melanoplus sanguinipes* (F.). and *Oedaleonotus enigma* (Scudder), are capable of attaining very high densities (>30/m^2). Both species feed upon a broad range of forbs (Brusven and Lamley 1971, Banfill and Brusven 1973, Sheldon and Rogers 1978). Pfadt (1992) suggested that an increase in introduced weeds is a factor leading to outbreaks of *O. enigma.* Fielding and Brusven (1993) found that both species prefer disturbed rangeland habitats dominated by exotic annual plants. This study assessed the utilization of diffuse knapweed as food by these 2 grasshopper species to determine if knapweed represents a significant and expanding resource for grasshoppers and if grasshopper herbivory may be a constraint to knapweed populations.

Previous studies (Brusven and Lamley 1971) have shown *Sisymbrium altissimum* L., an introduced annual forb, to be preferred by many forb-feeding grasshoppers. Both species of weeds initiate growth as a basal rosette of leaves and later develop erect, sparsely leaved stems that bear flowers. Because *C. diffusa* is usually a biennial, it does not develop beyond the basal rosette until the 2nd year. *Sisymbrium altissimum* constituted a large proportion of the forbs present in this study; therefore utilization of *C. diffusa* and *S. altissimum* was compared.

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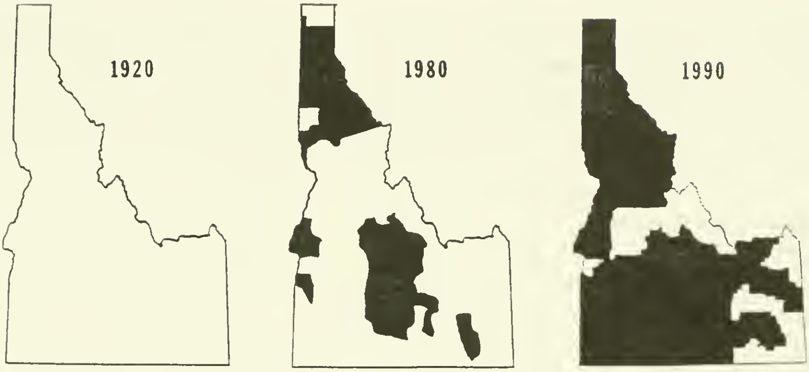

Fig. 1. Idaho counties reporting infestations of diffuse knapweed, *Centaurea diffusa*.

MATERIALS AND METHODS

The study site is about 3 km south of Shoshone, Idaho (Lincoln County), in a knapweed-infested area that had been seeded with crested wheatgrass (*Agropyron cristatum* [L.] Gaertn.) in 1975. Grasshopper food preferences were identified by microhistological analysis of grasshopper crop contents (Brusven and Mulkern 1960, Sparks and Malechek 1968, Fielding and Brusven 1992). Grasshoppers were confined to cages so that relative amounts of different plant species could be precisely determined. Five trials were conducted during the summer of 1989: *O. enigma* 4th- and 5th-instar nymphs in early June; *O. enigma* adults and *M. sanguinipes* 4th and 5th instars in late June; *M. sanguinipes* adults in July and again in August. For each trial, 4 wire-mesh (5-mm pore size), conical cages covering 0.5 m^2 each were placed in the field such that at least 1 plant each of *C. diffusa* and *Sisymbrium altissimum* L., along with assorted common grasses, occurred within each cage. Twelve to 15 grasshoppers of a single species were placed in each cage. Grasshoppers used in the tests were collected from rangeland and placed in the cages within 20 h of collection. A 4-d interval was estimated to be sufficient to completely void previous meals and to accurately assess preferences in choice tests. After 4 d, 10 grasshoppers were removed from each cage and immediately preserved in 95% ethanol for crop analysis.

Species composition of plants in each cage was determined on an air-dry basis by clipping and sorting by species aboveground portions of plants in each cage after each trial. Clipped plants were stored in air-tight plastic bags, and fresh weight was obtained within 4 h of clipping. Clipped plants were then allowed to air-dry until they quit losing weight (10–15 d), after which dry weights were obtained (to the nearest 0.1 g). Percent moisture of aboveground portions of each plant species was then determined.

Plants were rated after each trial according to phenology as follows: 1, vegetative growth only; 2, flowering; 3, seed set; 4, seed maturity; 5, senescent or dormant (USDA–Soil Conservation Service 1976). Grass species present included *Poa sandbergii* Vasey, *Bromus tectorum* L., and *Agropyron cristatum*. *Centaurea diffusa* and *S. altissimum* composed about 97% of aboveground biomass of forbs. Both 1st- and 2nd-year *C. diffusa* were present in each of the cages. Other forbs present were *Helianthus annuus* L., *Lactuca serriola* L., and *Epilobium* L. sp.

Grasshopper crops were removed and the contents mounted on glass slides in glycerin and safranin stain. Plant fragments in the crops were identified by comparing them with reference slides made from fragments of known plants collected at the study site, similar to the methods described by Fielding and Brusven (1992). Frequency counts were made for each plant species by determining their presence or absence in 20 microscope viewing fields per grasshopper crop. Trichomes, hairs, and pollen were not counted. Frequencies from the 10 grasshoppers per cage were summed. Relative frequency was calculated by dividing the frequency of a plant species by the total frequency of all plant species (Sparks and Malechek 1968, Pfadt and Lavigne 1982). Holecheck and Gross (1982) demonstrated the near equivalence of relative frequency to actual dry weight percentage of plants consumed.

Relative availability of different plant species within an area has been shown to influence diet composition in many grasshopper species (Ueckert et al. 1972, Mitchell 1975). To account for the effect of availability on consumption, preference values for plant species constituting more than 10% of either cage or crop contents were calculated by dividing relative frequency of a plant species in the crops by that species' percentage of the dry-weight of all plants within the cages (Ueckert and Hansen 1971). A preference value >1 indicates feeding in greater proportion to the plant's availability, whereas a preference value <1 indicates low preference in relation to a plant's availability.

Possibly, total dry weight of a plant may not accurately portray the amount of plant material available to grasshoppers, thus introducing bias into the preference values. In this study our observations indicated that both species of weeds had similar ratios of leaves to stems. Also, we have observed grasshoppers feeding on stems of both weed species. Because we had no way to determine more precisely exactly what proportion of the plant was available as food to the grasshoppers, we used total aboveground biomass as a reasonably objective measure of availability. The presence of 1st-year rosettes of *C. diffusa* in the cages ensured that each replication included a representative choice of plant material.

Differences between plant species in relative frequency and preference values were tested using the Wilcoxon 2-sample test (PROC NPAR1WAY, SAS 1985), with each cage representing 1 replication. Comparisons between plant species were made for each trial of a single grasshopper species and with data from different trials pooled by grasshopper species. The same statistical methods were also used to test for differences in relative frequency and preference values between grasshopper species for *C. diffusa* and *S. altissimum*.

Food selection was monitored in an uncaged population of *M. sanguinipes* near the cage study. Thirty to 50 individuals were collected on each of 5 dates from June through October from an area of ca 1 ha infested with knapweed. Food preference in this population was determined by microhistological methods described above.

Plant species composition at the site was determined by visual estimates, in 5% increments, of the ground cover of each plant species in forty 0.1-m^2 quadrats, arranged in 4 transects of 10 quadrats each. Ground cover estimates were made in July and again in October after precipitation caused abundant germination of cheatgrass. Because accurate estimates of food availability (biomass) in the field were not available, preference values were not calculated and the results are presented for comparative purposes only.

RESULTS

Cages were placed such that *C. diffusa* was equally as abundant as or more abundant than *S. altissimum* in each trial (Table 1). Percentage moisture of both species of weeds declined throughout the season (Table 1). *Sisymbrium altissimum* tended to be slightly more advanced phenologically than *C. diffusa* throughout the season, partly due to the presence of 1st-year rosettes of *C. diffusa* in the cages, but also because of earlier flowering by *S. altissimum* (Table 1).

Although *C. diffusa* constituted a substantial percentage (10–46%) of the caged grasshoppers' diet, preference values for *C. diffusa* were <1 in every trial, indicating that it was not consumed in proportion to its dry weight composition within the cages (Table 1). Preferences values for *S. altissimum* were >1 in each trial, indicating that it was consumed in proportions greater than its relative availability.

After flowering in July, a large portion of the *C. diffusa* plant material in the crops of *M. sanguinipes* consisted of floral parts (44% and 30% of the *C. diffusa* material consumed, in the July and August trials, respectively). Other forbs represented in in situ caged trials were not present in sufficient quantity to adequately assess their preference values.

More *S. altissimum* than *C. diffusa* was consumed by grasshoppers in 3 of the 5 trials (Table 1). Preference values for *S. altissimum* were greater than those for *C. diffusa* in 4 of the trials (Table 1). Combining data from the 3 trials with *M. sanguinipes*, crop contents and preference values for *S. altissimum*, 42% and 2.0, respectively, were greater than for *C. diffusa*, 16% and 0.5, respectively (Wilcoxon test, $P < 0.01$ for both tests). For *O. enigma*, the overall preference value for *S. altissimum*, 3.5,

TABLE 1. Relative availability and consumption by grasshoppers of plant species.

Plant species	Plant phenological stage[1]	Percent moisture of plants	Mean dry weight in cages	Relative availability in cages[2]	Relative frequency in crops	Mean preference index
4th- and 5th-instar *Oedaleonotus enigma* nymphs on 6 June 1989						
Centaurea diffusa	1	77	13.4	23	10a[3]	0.38a
Sisymbrium altissimum	1	81	8.8	15	48b	5.06b
Other forbs	1	85	0.6	1	<1	—
Agropyron cristatum	1–2	57	18.1	31	<1	<0.05
Poa sandbergii	4	24	4.7	8	2	—
Bromus tectorum	4	21	12.8	22	32	1.42
Detritus					6	
adult *Oedaleonotus enigma* on 26 June 1989						
Centaurea diffusa	1	64	59.0	61	46a	0.76a
Sisymbrium altissimum	1–2	67	27.1	28	48a	1.93a
Other forbs	1–2	79	1.0	1	1	—
Agropyron cristatum	3–4	45	6.8	7	0	—
Poa sandbergii	5	15	0	0	0	—
Bromus tectorum	5	12	3.6	3	1	—
Detritus					4	—
4th- and 5th-instar *Melanoplus sanguinipes* nymphs on 26 June 1989						
Centaurea diffusa	1	64	60.8	59	16a	0.25a
Sisymbrium altissimum	1–2	67	25.8	25	74b	3.00b
Other forbs	1–2	79	2.1	2	0	—
Agropyron cristatum	3–4	45	6.2	6	0	—
Poa sandbergii	5	15	4.1	4	5	—
Bromus tectorum	5	12	3.1	3	4	—
Detritus					2	—
adult *Melanoplus sanguinipes* on 21 July 1989						
Centaurea diffusa	1–2	63	25.4	29	16a	0.56a
Sisymbrium altissimum	2–3	55	24.5	28	44b	1.55b
Other forbs	1–2	75	8.8	1	3	—
Agropyron cristatum	4	45	7.0	8	4	—
Poa sandbergii	5	9	17.5	20	3	0.17
Bromus tectorum	5	14	11.4	13	27	2.52
Detritus					3	—
adult *Melanoplus sanguinipes* on 25 August 1989						
Centaurea diffusa	1, 3–4	22	38.8	38	23a	0.70a
Sisymbrium altissimum	4–5	11	18.4	18	24a	1.48b
Other forbs	2–3	65	8.2	8	5	—
Agropyron cristatum	4	18	15.3	15	3	0.37
Poa sandbergii	5	8	4.1	4	5	—
Bromus tectorum	5	7	13.3	13	25	2.83
Detritus					16	—

[1] 1, vegetative growth only; 2, flowering; 3, seed set; 4, seed maturity; 5, senescent or dormant

[2] Mean ($N = 4$) percentage of aboveground plant biomass (air-dry basis) within cages

[3] Means for *C. diffusa* and *S. altissimum* within columns of each trial followed by different letters are significantly different, $P < 0.05$, Wilcoxon 2-sample test.

was greater than for *C. diffusa*, 0.6 (Wilcoxon test, $P < 0.05$). There was no difference in consumption by *O. enigma* between *S. altissimum* and *C. diffusa*, 48% and 27%, respectively (Wilcoxon test, $P > 0.05$). There were no differences between the 2 species of grasshoppers in relative frequency or preference values for either *S. altissimum* or *C. diffusa* (Wilcoxon test, $P > 0.10$ for both comparisons).

Of the grass species, only *Bromus tectorum* was eaten in greater proportion than its percentage of air-dry biomass. Even though *O. enigma* is generally considered to be a forb-feeder (Sheldon and Rogers 1978, Pfadt 1992), *B. tectorum* constituted 32% of the diet of *O. enigma* in early June (Table 1). Adult *O. enigma* in late June ate very little *B. tectorum*. *Melanoplus sanguinipes* consumed *B. tectorum* throughout the summer, with 4–27% of its diet composed of *B. tectorum*, even though the grass was completely senescent by 26 June (Table 1).

TABLE 2. Relative frequency of food items in crops of *M. sanguinipes* on 5 dates and percentage ground cover in July and October 1989.

	Relative frequency of crop components					Percentage ground cover	
	30 June	20 July	14 Aug	6 Sep	13 Oct	July	October
Sisymbrium altissimum	46	23	22	7	6	2	1
Centaurea diffusa	18	30	32	55	1	6	4
Other forbs[a]	19	25	7	24	6	<1	<1
Bromus tectorum	7	9	12	6	76	5	16
Other grasses	1	4	15	1	10	5	6
Litter, detritus	9	9	13	7	1		

[a] Includes rabbitbrush (*Chrysothamnus nauseosus* [Pall.] Britt.), lupine (*Lupinus* L. sp.), and sunflower (*Helianthus annuus* L.)

Knapweed was the most common forb growing on the site where the uncaged population of *M. sanguinipes* was studied (Table 2). In June, *S. altissimum* was the largest single food item, but consumption declined as the season progressed. Knapweed was a substantial food item, especially in August and September when it remained succulent after other forbs had dried. After rainfall stimulated germination of *B. tectorum* in late September and October (Table 2), it became the primary food item for *M. sanguinipes*, and forbs constituted only a minor portion of the diet.

DISCUSSION

The evolutionary history of an herbivorous species, by shaping its food habits and other life history traits, determines its present relationships with exotic plant species. The 2 grasshopper species in this study consume a wide variety of plants, especially forbs (Banfill and Brusven 1973, Sheldon and Rogers 1978, Pfadt 1992), and will readily accept exotic plant species. *Melanoplus sanguinipes* is a very opportunistic feeder. Egg hatch in this species is often spread out over a long period, resulting in a large proportion of a population maturing during the dry periods typical of late summer in the intermountain region. At such times many late-maturing plants that still retain some succulence, such as rabbitbrush, sagebrush, and some lupine species, are primary food items for *M. sanguinipes*. The results of this study indicate that this was the case with *C. diffusa*; even though it was not highly preferred by *M. sanguinipes*, it was a major food item in late summer when most other plants were dry. *Sisymbrium altissimum* tended to become senescent earlier than *C. diffusa*, which would reduce the quality of *S. altissimum* relative to *C. diffusa*, especially when 1st-year rosettes, consisting mostly of leaves, are considered.

Locken and Kelsey (1987) reported that cnicin concentrations in *C. maculosa* vary considerably within and among individual knapweed plants. Cnicin is stored within glandular trichomes on the surface of knapweed tissues. Highest concentrations of cnicin were found in leaves surrounding the inflorescence. Only trace quantities were found by Locken and Kelsey (1987) in the stem epidermis and flowers. Leaf concentrations were lowest in spring and increased with flowering. We assume that cnicin concentrations in *C. diffusa* follow much the same pattern. Variability in cnicin concentration may result in selective consumption by grasshoppers of knapweed tissues with low cnicin concentrations. Our results suggest that this is the case: In late-summer trials much of the knapweed tissue consumed by grasshoppers consisted of flowers. This implies that during years of high grasshopper densities, feeding by grasshoppers, especially on the flowers, could result in a modest reduction in seed production in this plant.

Results of this study provide support for the hypothesis that knapweed is protected from herbivory by its chemical constituents (Picman 1986, Locken and Kelsey 1987). When compared to *S. altissimum*, diffuse knapweed was a 2nd-choice food item for these generalist grasshopper species. Its low palatability may confer a competitive advantage to knapweed when herbivory is a strong selection factor. Although it is conceivable that at high densities grasshoppers may consume significant amounts of knapweed and reduce seed production, many other plants would be affected to a greater degree, thus reducing competition to knapweed.

Grasshopper species used in this trial are the dominant species contributing to outbreaks in southern Idaho. It appears that increasing knapweed infestations do not represent a significant increase in food resources for these grasshoppers. However, because knapweed stays green longer during the summer than many other rangeland plants, it may provide sustenance for polyphagous grasshoppers during late-summer droughts in southern Idaho.

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FIRE FREQUENCY AND THE VEGETATIVE MOSAIC OF A SPRUCE-FIR FOREST IN NORTHERN UTAH

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ABSTRACT.—Fire scar and vegetative analysis were used to construct a fire history for the Engelmann spruce/subalpine fir (*Picea engelmannii/Abies lasiocarpa*) vegetation type of the Utah State University (USU) T. W. Daniel Experimental Forest. Three distinct periods of fire frequency were established—presettlement (1700–1855), settlement (1856–1909), and suppression (1910–1990). Mean fire interval (MFI) decreased during the settlement period and greatly increased during the suppression era. The difference was attributed to the influx of ignition sources during the settlement of nearby Cache Valley, located 40 km to the west. Logging and livestock grazing appear to have led to the reduced MFI, which in turn worked as a factor to create the vegetative mosaic now observed on the study area. The increase in MFI during the suppression era permitted the advancement of shade-tolerant species in the understory of the shade-intolerant lodgepole pine (*Pinus contorta* var. *latifolia*) and quaking aspen (*Populus tremuloides*). Continued suppression of disturbance from wildfire will allow the lodgepole pine cover type, which experienced the lowest MFI during the settlement period, to be further invaded by shade-tolerant species, decreasing spatial stand diversity and increasing the risk of more intense fires.

Key words: fire frequency, subalpine spruce-fir forest, fire scar.

Absence of natural fire in wildland ecosystems, due to removal of fine fuels by livestock, reduction in Native American ignitions, and a suppression policy instituted in the early 1900s has led to extensive alterations in natural vegetative succession patterns. Human disruption of natural fire regimes in fire-dependent communities limited natural diversity and altered the long-term stability of fire-adapted plant species (Heinselman 1973, Gruell 1986, Agee 1993). Previously, natural ecosystems had evolved under episodic fires (Parsons 1981, Gruell 1983). Gruell's (1983) interpretation of paired photos from the Northern Rockies showed early stages of forest succession were more common from 1870 to 1940 than they are today; however, Gruell (1983) also found the absence of fire has contributed to a marked alteration of natural vegetation mosaics by favoring woody species such as shrubs and trees over grasses.

Lightning-ignited fires in Engelmann spruce/subalpine fir (*Picea engelmannii/Abies lasiocarpa*) forests are less frequent than fires in drier vegetation types. Arno (1980) estimated a fire return interval of 50 to 130 yr for spruce/fir habitat types. Veblen et al. (1994) found a mean fire-return interval of ca 200 yr in a Rocky Mountain subalpine forest in northwestern Colorado. In these subalpine fir forests, historic fire allowed the dominance of seral species and created a mosaic of species and age compositions. Where seral species such as lodgepole pine (*Pinus contorta*) or aspen (*Populus tremuloides*) occurred, a higher fire frequency favored their dominance (Bradley et al. 1992). In the lodgepole pine–dominated communities that occur in the lower portion of the subalpine fir forest, fire was more frequent with intensity depending on amount of precipitation received in the summer months. Abundant evidence was found in the lodgepole pine forests of northern Utah of nondestructive ground fires, more intense "thinning" fires, "stand-replacing fires, and severe double burns" (Arno 1980).

Fire history studies provide land managers with estimates of past fire frequencies, mean fire-return intervals, and effects of natural fire on stand composition and structure (Arno and Sneck 1977). Such studies help to determine the return interval of fires on a site, intensity and size of fire, effects of past fire on stand dynamics, and effects of an era of modern suppression. Managers may also use the natural fire cycle or regime of an area to determine if the present disturbance regime is within the historical range of variation. A variety of techniques are used to evaluate fire history, including mapping stand types, correlating fire dates from fire-scarred trees to establish a fire chronology, and determining age-class distributions, using increment cores to establish the extent of fires (Arno 1980, Tande 1979).

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The objective of this study was to determine if the existing vegetative mosaic of the T. W. Daniel Experimental Forest is correlated with the fire history of the study area, primarily, whether fire frequency has changed between 3 distinct periods: presettlement, settlement, and suppression. Additionally, if fire frequency has changed, is that change reflected in the vegetation structure visible today.

STUDY AREA

The USU T. W. Daniel Experimental Forest, located about 40 km east of Logan, Utah, is 1036 ha in area and ranges in elevation from 2377 m to 2651 m (Fig. 1). Topography ranges from higher plateaus dissected by deep drainages to gentle slopes and small meadows. No permanent lakes or streams are within the study area (Schimpf et al. 1980); however, intermittent streams do carry runoff from the site. Winters are cold and wet, and summers are warm and dry. Mean annual precipitation is 104 cm per yr, mostly falling as snow (Hart and Lomas 1979).

The major vegetation component is the Engelmann spruce/subalpine fir type in late successional stages, with seral lodgepole pine (*Pinus contorta* var. *latifolia*) and quaking aspen stands, and small meadows distributed throughout. A young conifer understory consisting primarily of subalpine fir is often present in the aspen stands (Schimpf et al. 1980).

METHODS

Fourteen sampling transects were established along contours spaced 61 m apart based on slope distance. A continuous log of forest cover type, the predominant vegetative type, was kept along each transect to create a stand map. As the contour intervals were traversed, trees with fire scars were identified and recorded. The number of fire scars was recorded for each "catface"—an open scar resulting from fire damage. Fire scars are formed when flames near the trunk raise the temperature of the cambium to a lethal level, or actually consume bark, phloem, and xylem (McBride 1983). Trees with the largest number of sound scars were marked for further study.

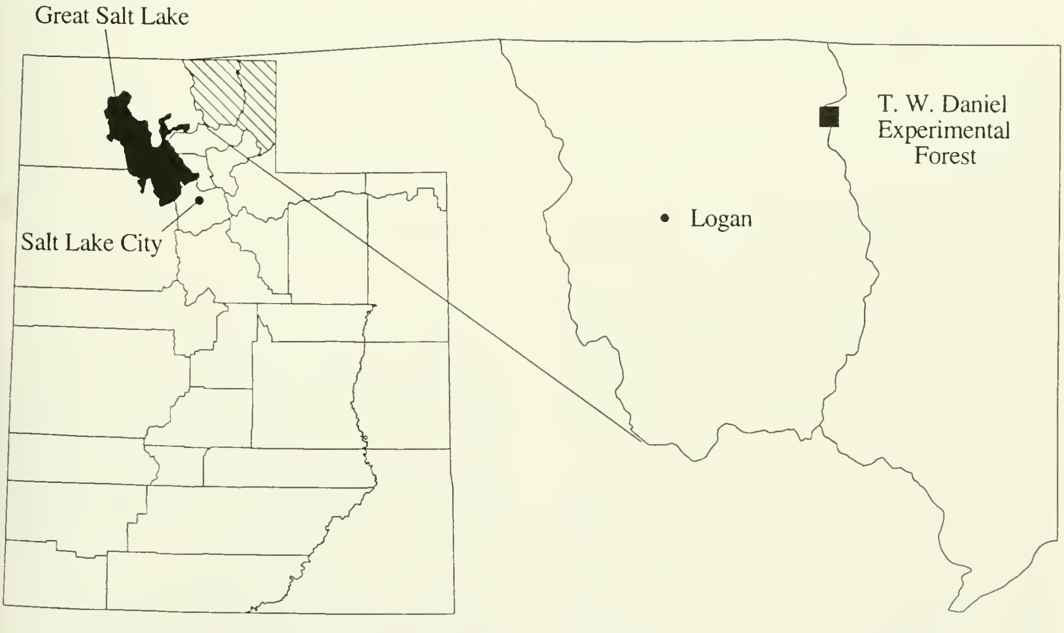

Fig. 1. Map showing approximate location of the T. W. Daniel Experimental Forest between Cache and Rich counties northeast of Logan, Utah.

Sixty-two trees with the greatest number of visible, individual fire scars were sampled by taking a partial cross section from the pith to 1 side of the catface (Arno and Sneck 1977). The wedges were sanded and annual growth rings counted, recording the number of years back to each fire and the number between fires. Trees may be scarred in a number of ways including mechanical damage by nearby falling trees, root rot infection, lightning, or strip attacks by mountain pine beetle (*Dendroctonus ponderosae* Hopkins, Coleoptera: Scolytidae) (Johnson and Gutsell 1994); however, there were no blue stains, larval galleries, or beetle emergence holes in the scars sampled (Stuart et al. 1983), which would suggest they had resulted from causes other than fire. Because pockets of obscured rings or rot may also cause inaccurate counts, tree records were combined into a master fire chronology (Arno and Sneck 1977).

Individual tree ring counts were arranged horizontally on paper, geographically ordered so that neighboring trees were adjacent. Ten-year increments were placed on the left vertical axis, beginning with the sample year at the top, and the oldest ring year recorded at the bottom. The number of trees scarred in a year was compared to the number of trees susceptible to scarring. If a tree was consistently out of order, a number of years was added or subtracted to bring it into alignment (Arno and Sneck 1977). The maximum number of years added or subtracted equaled 3; and 16 trees were adjusted.

Variable-radius plots were laid out along the sampling transects at a spacing of 200 m. Tree species present were recorded to determine cover type, and a site tree—a dominant or codominant tree on the plot—was aged for each species. Increment cores were taken at breast height for each site tree and were adjusted for total age for each species. A 740th-ha regeneration plot was recorded, tallying seedlings and saplings by species and diameter, at the center of the variable plot to aid in determining successional patterns.

Cover type, dated scars, and stand age data collected from these plots were incorporated into a stand map to show the extent of stands that might have resulted from a fire disturbance (McBride 1983). The stand map was supplemented by remotely sensed satellite imagery obtained in 1986.

Fire frequency, "the number of fires per unit of time" (Romme 1980), on an area was calculated for 3 fire frequency periods to portray the effects of settlement, logging, grazing, and modern fire suppression on the fire regime. Mean fire intervals, "an arithmetic average of all fire intervals determined in a designated area" (Romme 1980), were calculated for each period. Determining mean fire intervals for distinct land-use periods is useful in understanding human impact on forest ecology and fire history (McBride 1983). The periods were "suppression" (1910–1990), when U.S. Forest Service fire suppression was initiated, "settlement era" (1856–1910), and "presettlement" (prior to 1856). Mormon pioneers established the first settlement by Europeans in the Cache Valley in 1856 (Bird 1964). The presettlement period began the year just prior to the age of the oldest tree sampled—1700 (Romme and Despain 1989). A fire history is limited by longevity of trees on the site and durability of wood exposed when scarred (Heinselmann 1973).

Total number of years in each period was then divided by the number of fires in that period to obtain mean fire interval. Documented evidence of historical fires was used to verify dates in the settlement-era and fire-suppression periods (Bird 1964).

A master fire chronology was developed for each stand experiencing fire in the study area as indicated by scars and the presence of even-aged stands of lodgepole pine (Romme and Despain 1989) or aspen stands (Brown and Simmerman 1986, Debyle et al. 1987). Stands were considered even-aged if deviation in the increment core age of site trees was ≤ 20% (Daniel et al. 1979).

RESULTS

Three forest cover types consisting of 15 stand types were identified. Species represented in pure stands were lodgepole pine, Engelmann spruce, subalpine fir, and quaking aspen, but the area in pure stands was relatively small compared to that of mixed stands: 280 ha in pure stands versus 580 ha in mixed stands out of a total 1036 ha.

Of the 15 delineated stand types, subalpine fir, the climax species in the habitat type present (Schimpf et al 1980), was a major secondary stand component in 9 types and the

TABLE 1. Percent of regeneration by species within stand type. Subalpine fir is the primary component in regeneration in all stands except aspen.

Stand type	Subalpine fir	Engelmann spruce	Aspen	Lodgepole pine	Douglas-fir
DF/PF[a]	100	0	0	0	0
DF/ES/AF	100	0	0	0	0
LP	75	19	6	0	0
LP/AF/AS	67	11	22	0	0
DF/AF	67	33	0	0	0
DF/ES	67	33	0	0	0
LP/AF	65	35	0	0	0
LP/AF/ES	61	31	0	8	0
ES	60	25	15	0	0
ES/AF	57	32	11	0	0
AF	56	33	11	0	0
AF/AS	52	0	48	0	0
AS/ES/AF	46	27	27	0	0
AS	41	3	53	0	3

[a] Stand type abbreviations: AF = subalpine fir, AS = aspen, ES = Engelmann spruce, LP = lodgepole pine, DF = Douglas-fir, PF = limber pine.

principal component in 2. Regeneration surveys conducted at each plot showed subalpine fir to be the primary regeneration component in 13 of the 15 types (Table 1). Aspen regeneration was the primary component in the aspen stand type. Overstory ages ranged from 63 to 284 yr in lodgepole pine, 106 yr in aspen, 188 yr in subalpine fir, and 193 yr in Engelmann spruce.

Sixty-two fire-scar wedges were collected from fire-scarred trees, 22 from Engelmann spruce, 1 from subalpine fir, and 39 from lodgepole pines. All scar and pith dates were used in the master fire chronology, but only 6 of the spruce scars were used to indicate fire years, while 37 lodgepole pine scars were utilized. The remaining scars were not used due to rings obscured by decay.

Sixteen fire years were represented in scar and/or regeneration data. Where scars were not present, but vegetation was even-aged, e.g., stands L20, F24, L18, and L17 (Tables 2, 3), a fire year was determined from the age of dominant lodgepole pine or aspen trees present. Two of the 16 fire years, 1700 and 1860, were represented solely by age-classes on the site. Two fire years during the settlement period, 1890 and 1895, were documented by Bird (1964). Bird's account stated that numerous small fires were reported in Logan Canyon in 1890, while the 1895 fire year was substantiated by a large fire reported in Stump Hollow in Logan Canyon, an area north of the study area (Bird 1964).

Those stands where the major component was lodgepole pine exhibited 13 fire years, 4 in the presettlement fire period from 1700 to 1855, 9 in the settlement period from 1856 to 1909, and no fires in the suppression period from 1910 to the present. Ten of the 13 fires were represented by fire scars in the present stands (Table 2).

There were 7 fire years in stands in the spruce/fir cover type, which predominantly comprised spruce/fir and secondary components of lodgepole pine, aspen, Douglas-fir, and limber pine. There were no fires in the presettlement period, 6 in the settlement period, and 1 in the suppression period. Five of the 7 fires were recorded by scars and validated by age of the present stand (Table 3). There were 4 fire years in the aspen cover type. Three of those fires were validated by both fire scars and age-class analysis. One fire occurred in the presettlement period and 4 in the settlement period (Table 3). Only 1 fire year, 1903, was common to all 3 forest types. Four fire years (1860, 1890, 1902, and 1903) were shared between the spruce/fir and lodgepole pine cover types (Figs. 2, 3).

Mean fire intervals estimated for the entire study area, for each cover type, and for each fire frequency period are shown in Table 4. Mean fire interval for the entire study area was 18 yr, i.e., a fire occurred about every 18 yr somewhere within the study area. Mean fire interval was shortest in lodgepole pine and longest in aspen. During the presettlement

TABLE 2. Fire frequency in the lodgepole cover type by stand and fire year. Stands consist of a predominant lodgepole component or mixed species with the primary overstory component of lodgepole pine. (Adapted from Arno and Sneck 1977.)

Fire	Stands															
year	L2[a]	L3	L4	L5	L6	L7	L22	L11	L10	L12	L15	L20	L18	L17	L9	L13
Suppression period																
1942	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Settlement period																
1909	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
1903	3r[b]	2r	1r	4r	2	1	1	–r	—	—	—	—	—	—	—	—
1902	—	—	—	—	—	—	—	1r	1	1r	1	1r	1	5r	—	—
1899	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
1895	–r	—	—	—	—	1	—	—	—	—	—	—	—	—	–r	—
1890	—	—	—	—	—	—	—	—	1	–r	–r	—	—	—	—	–r
1887	—	—	—	–r	—	—	—	—	—	—	—	—	—	—	—	—
1883	–r	—	—	1r	—	—	—	—	—	—	—	—	—	—	—	—
1877	–r	—	—	–r	—	1	—	—	—	—	—	—	—	—	—	—
1860	—	—	—	—	—	—	—	—	—	—	—	–r	–r	–r	—	—
1858	—	—	—	—	—	—	—	—	2	—	—	—	—	—	—	—
Presettlement period																
1847	–r	–r	—	2r	—	—	—	—	—	—	—	—	—	—	—	—
1834	—	—	—	—	—	—	—	—	1r	—	—	—	—	—	—	—
1822	—	—	—	—	—	—	—	—	1r	—	—	—	—	—	—	—
1700	—	—	—	r	—	—	—	—	—	—	—	—	—	—	—	—

[a] Stand description: Lodgepole = L3, L5, L6, L22, L12, L17, L9, L13; LP/AF/AS = L2, L7, L15; LP/AF = L4, L11, L20; LP/AF/ES = L10, L18. LP = lodgepole pine, AF = subalpine fir, AS = aspen, ES = Engelmann spruce.

[b] Digit (1,2, etc ...) = number of trees in stand with fire-scar date; r = regeneration in stand, determined from increment cores.

TABLE 3. Fire frequencies in the Engelmann spruce/subalpine fir and aspen cover types. (Adapted from Arno and Sneck 1977.)

Fire	Engelmann spruce/subalpine fir stands							Aspen stands	
year	E2[a]	E4	E5	F21	F24	F7	F23	A3	A8
Supression period									
1942	1[b]	—	—	—	—	—	—	—	—
Settlement period									
1909	—	—	—	—	—	—	1	—	—
1903	1r	1r	2r	—	—	—	—	1	1r
1902	1	—	—	–r	1	—	—	—	—
1899	1	—	—	—	—	—	—	—	—
1895	—	—	—	—	—	—	—	—	—
1890	—	—	—	—	—	–r	—	—	—
1887	—	—	—	—	—	—	—	1r	—
1883	—	—	—	—	—	—	—	1	—
1877	—	—	—	—	—	—	—	1	—
1860	—	—	—	—	–r	—	—	—	—
1858	—	—	—	—	—	—	—	—	—
Presettlement period									
1847	—	—	—	—	—	—	—	–r	—
1834	—	—	—	—	—	—	—	—	—
1822	—	—	—	—	—	—	—	—	—
1700	—	—	—	—	—	—	—	—	—

[a] Stand description: ES/AF = E2, E5, AF/AS = F3, F23; DF/ES = D2; AF/LP = F5, F7; ES/AF/AS = E4, F24, AF/ES = F9, AF/LP/ES = F21; AS = A3, A8. AS = aspen, AF = subalpine fire, DF = Douglas-fir, ES = Engelmann spruce, and LP = lodgepole pine.

[b] Digit (1, 2) = number of trees in stand with fire-scar date; r = regeneration in stand determined from increment cores that correspond to fire data.

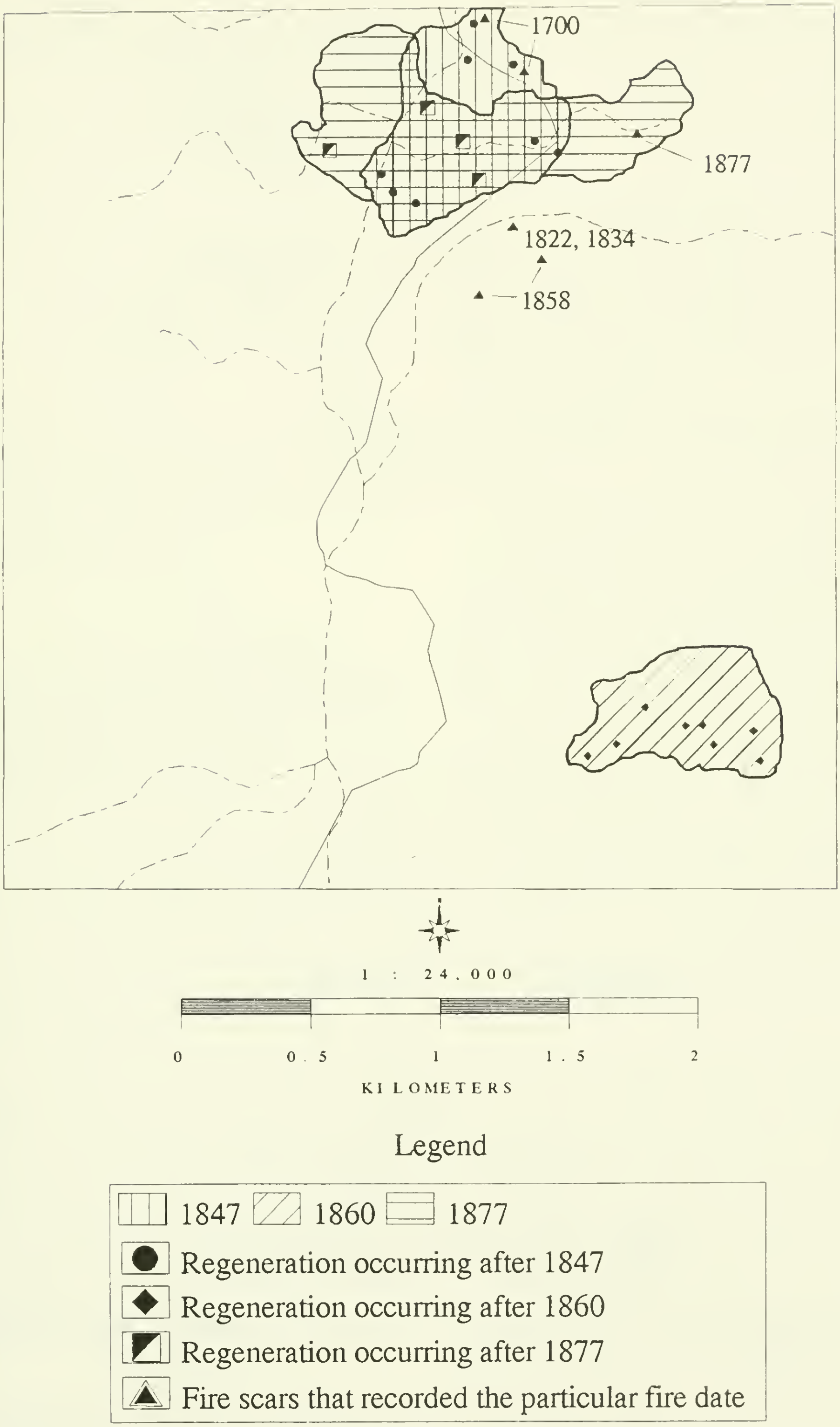
1700
1877
1822, 1834
1858
1 : 24,000
0
0.5
1
1.5
2
KILOMETERS
Legend
1847
1860
1877
Regeneration occurring after 1847
Regeneration occurring after 1860
Regeneration occurring after 1877
Fire scars that recorded the particular fire date

Fig. 2. GIS-produced diagram of fires in the study area from 1700 through 1877 based on stand mapping, regeneration, and fire-scar data.

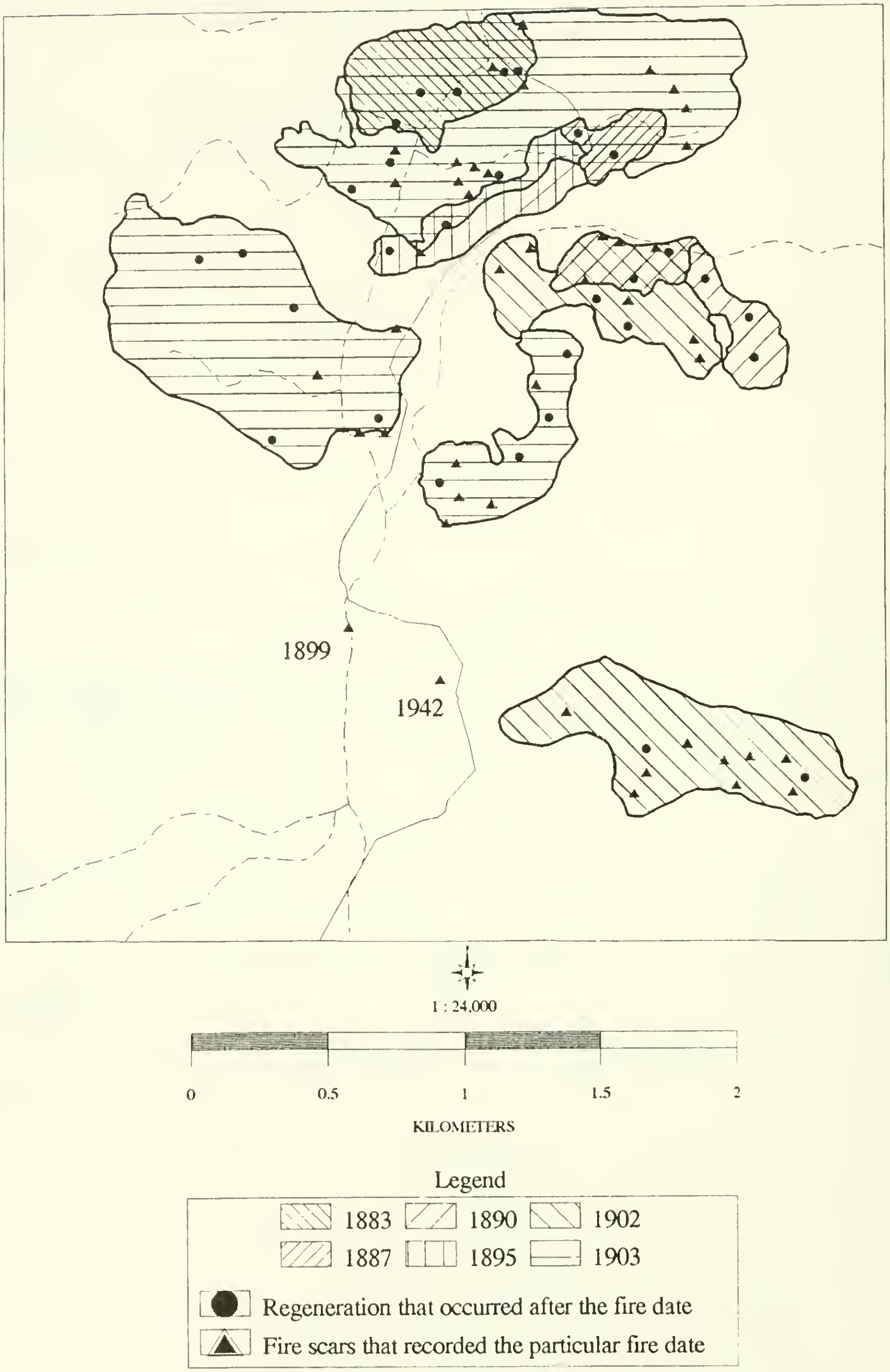
1899
1942
1 : 24,000
0
0.5
1
1.5
2
KILOMETERS
Legend
1883
1890
1902
1887
1895
1903
Regeneration that occurred after the fire date
Fire scars that recorded the particular fire date

Fig. 3. GIS-produced diagram of fires in the study area from 1883 through 1942 based on stand mapping, regeneration, and fire-scar data.

TABLE 4. Mean fire interval by cover type and fire frequency period. Mean fire interval is an arithmetic average in years of the number of years in a period divided by the number of fires occurring in that period. A double hyphen denotes that no evidence of fire occurring in that period was found. Ranges of intervals are in parentheses.

	Presettlement (1700–1855)	Settlement (1856–1909)	Suppression (1910–1988)	Total (289 years)
Study area	39 (1–122)	4.9 (1–30)	79	18.1
Cover types				
ES/AF	—	9 (1–30)	79	41.3
LP	39 (12–122)	6 (1–17)	—	22.2
AS	156	13.5 (4–16)	—	57.8

and settlement periods, mean fire interval was shortest in lodgepole pine. Mean fire intervals were longest in the suppression period (e.g., spruce/fir) or no fires occurred (e.g., lodgepole pine and aspen; Table 4).

DISCUSSION

Stand Age and Regeneration

The widespread occurrence of subalpine fir in the cover types, both in the overstory component and in the regenerating understory, is associated with later stages of succession (Schimpf et al. 1980). Stands sustaining the most recent extensive fires, 1902 and 1903, have less of a subalpine fir component than those not withstanding recent fires (Figs. 2, 3). However, subalpine fir is apparent as a component of regeneration following these fires and now as a tolerant understory.

Fire frequencies declined during the last century, a trend that would favor the establishment of stands of Engelmann spruce and subalpine fir that are less resistant to fire. When a subalpine fir climax is reached, overtopping intolerant seral species, it is not easily replaced due to its tolerant reproduction, unless a disturbance interferes, such as fire, insects, disease, or logging (Eyre 1980). Aspen stands also have a component of subalpine fir present and will require a disturbance if they are not to be replaced by the tolerant subalpine fir climax (Mauk and Henderson 1984).

Fire Frequencies

Compared to the mean fire interval in the presettlement period, there was a large increase in fire frequency in the settlement period in all 3 cover types (Tables 2, 3). Both Bird (1964) and Roberts (1968) stated that ignition sources increased while settlement was occurring in Cache Valley.

Size and number of fires in the mountains surrounding Cache Valley coincided with the heaviest use period (Bird 1964). The 1880 census stated 1%–10% of the timbered area of Cache County burned, or 5000 to 50,000 acres. Heavy grazing of the period undoubtedly reduced fine fuel loads, but use by loggers and sheepherders increased ignition hazards.

Fires were largely untended until 1906, when the U.S. Forest Service arrived. An employee of the U.S. Forest Service in 1906 stated that 3/4 of the Bear River Forest Reserve (later to become part of the Wasatch-Cache National Forest) had been burned over in the last 20 yr, probably due to careless sheepherders (Bird 1964). Fires were recorded in Blacksmith Fork Canyon in 1878, as well as a "large fire" in Stump Hollow in Logan Canyon in 1881 (Bird 1964).

Compared to the settlement period, fire frequency decreased during the suppression period and there was no evidence of fire in the lodgepole pine and aspen types. Forest Service suppression techniques decreased the size and occurrence of fires, which also coincided with a large reduction in allowable grazing, lessening an ignition hazard (Bird 1964).

The lack of evidence of fire since 1910 cannot be attributed to deterioration of fire-scar evidence. A fire severe enough to scar standing trees should be recorded in the present stands. The actual fire frequency may be higher than recorded; fires may not have been severe enough to scar trees (Lorimer 1984) or were suppressed before they became extensive.

Mean fire intervals in all cover types decreased in the settlement period and increased or there were no fires during the suppression era (Table 4).

There were few if any fires found in this study in the presettlement period. The fire scars in aspen may have been lost to natural mortality and decay, and fires may not have been severe enough to produce fire-scarred trees. Evidence of additional fires in the lodgepole pine and spruce/fir cover types may also have been destroyed, and actual mean fire intervals for this period may be substantially shorter.

Fire hazard in a lodgepole pine stand is highest shortly following a fire due to standing snags and remaining ground fuels from the previous fire, and later when crowns of the tolerant understory reach into crowns of mature lodgepole pine creating ladder fuels (Brown 1975, Romme 1982). In the study area, less fire-resistant Engelmann spruce and subalpine fir have begun to reach into the crowns of the lodgepole pine and aspen stands, increasing fire hazard. Both spruce and fir are highly susceptible to fire, due to their low-branching habits and thin bark (Schimpf et al. 1980). Evidently, fuel was also available to allow several nonlethal fires to burn in lodgepole pine stands, as occurred between 1877 and 1903 in the study area. One stand apparently burned 4 times during this 26-yr period, and several areas burned more than once (Table 2).

CONCLUSIONS

The lack of disturbance by fire on the USU T. W. Daniel Experimental Forest in the last 80 yr has allowed succession to proceed towards a climax of subalpine fir. The increase in fire frequency following settlement was probably due to efforts to exploit natural resources and the concomitant increase in ignition sources.

Frequent disturbance by fires during the settlement period resulted in the present mature vegetative mosaic. These earlier frequent fires favored lodgepole pine, and the less-frequent fires of the suppression period favored more tolerant species, as demonstrated by the abundance of subalpine fir regeneration in all cover types. The continued lack of disturbance will allow the more tolerant species of subalpine fir and Engelmann spruce to overtop the intolerant lodgepole pine and aspen. Eventually the area will lose its diverse appearance and will be similar to that in the areas where fire disturbance is less frequent.

ACKNOWLEDGMENT

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ARIZONA DISTRIBUTION OF THREE SONORAN DESERT ANURANS: *BUFO RETIFORMIS, GASTROPHRYNE OLIVACEA,* AND *PTERNOHYLA FODIENS*

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ABSTRACT.—We surveyed historic collecting localities in south central Arizona during July, August, and September 1993–94 to determine the presence of 3 little-known Sonoran Desert anurans, *Bufo retiformis, Gastrophryne olivacea,* and *Pternohyla fodiens.* All 3 species were present at most historic localities visited under appropriate conditions (following rainfall in July and August). *Pternohyla fodiens* was restricted to San Simon Wash and associated tributaries in south central Pima County. *Gastrophryne olivacea* ranged from Vekol Valley in extreme southern Maricopa County south to the Mexican border, and southeast near Tucson and Nogales in Pima and Santa Cruz counties. *Bufo retiformis* occurred over the widest area, from southern Rainbow Valley in Maricopa County southwest to the vicinity of Organ Pipe Cactus National Monument, and southeast to the vicinity of Tucson and Sasabe in Pima County.

Key words: Bufo retiformis, Gastrophryne olivacea, Pternohyla fodiens, *historic distribution, present distribution, amphibian decline, Arizona, Sonoran Desert.*

Three relatively little-known anurans, *Bufo retiformis, Gastrophryne olivacea,* and *Pternohyla fodiens,* occur in the Sonoran Desert in south central Arizona. Although placed in separate families (Bufonidae, Microhylidae, and Hylidae, respectively), they are superficially similar in behavioral ecology. Each is inactive for more than 10 mon each year, emerging only to reproduce and forage following intense rainfall during the summer "monsoon" season. All exhibit "explosive" breeding behavior (Wells 1977) in which males form high-density aggregations for a few nights (sometimes only one) following a major rainstorm and call to attract females. Within Arizona all 3 species are largely restricted to a small portion of the Sonoran Desert in the extreme south central part of the state, so it is perhaps not surprising that they are relatively unknown. Indeed, *Bufo retiformis* was described in 1951 based on specimens collected southeast of Ajo in 1948 (Sanders and Smith 1951), and *Pternohyla fodiens* was first documented in Arizona in 1957 (Chrapliwy and Williams 1957, Williams and Chrapliwy 1958).

Given limited information on these Arizona anurans, this investigation was undertaken in 1993 and 1994 to ascertain their present distribution in Maricopa, Pima, Pinal, and Santa Cruz counties, Arizona. First, we describe methods used in conducting the survey. Then, for each target species surveyed, we describe distinguishing acoustic characteristics and outline historic and present distributions. Last, we present observations on breeding behavior.

MATERIALS AND METHODS

Survey Methods

All surveys were conducted along paved roads throughout the known ranges of the 3 target species following rainstorms during July, August, and September 1993–94. Given the highly unpredictable and variable nature of summer rainfall and the need for monitoring the entire south central portion of Arizona, we could only crudely estimate (e.g., weather reports) the appropriateness of field conditions (i.e., level of rainfall) for anuran activity prior to each field excursion. Whenever sufficient rainfall appeared to have fallen in the study area, we traveled to that particular area on the night of the rainfall event, or the following night, to survey for amphibians along roadways. Frequently, 2–3 nights of surveying occurred for each rainfall event. Occasionally, survey plans were adjusted to take advantage of local conditions (e.g., localized flooding).

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To conduct surveys we drove slowly (40–65 kmph) along paved roadways scanning for anurans on the road surface and listening for chorus activity adjacent to the roadway. Most roads in the study area are located in valley floodplains crossed by numerous washes so that collection of large rain pools immediately adjacent to roadways occurs commonly. If insufficient rainfall had occurred so that anuran surface activity was initiated but no chorusing activity was apparent (i.e., no calling or breeding), we continued driving, scanning for and recording all anurans found on the road. When activity was relatively high (e.g., >20 anurans/km) and/or associated with an area of interest (e.g., historic or suspected locality for one of the target species), we recorded every individual anuran seen on the roadway (for a minimum of 1 km) until lack of moisture resulted in reduced anuran activity (e.g., <5 anurans/km).

Whenever we detected chorusing activity or pools of water along the roadway, we stopped and scanned the area adjacent to the roadway. If none of the target species were detected either visually or acoustically, we resumed the road survey. If target species were present, we attempted to record a series of voucher calls (see below) and collect a small series of voucher specimens ($N < 10$). Unfortunately, summer rainfall in south central Arizona was below average during the survey period, resulting in few actual breeding aggregations. All specimens are deposited in the ASU Vertebrate Collection.

Field Observations

Each target species possesses distinctive vocalizations. Advertisement calls were recorded in the field with a Marantz PMD 430 stereo recorder and Sennheiser ME 80 microphone with K3-U power module, or a Sony WM-D6C cassette recorder and Sony ECM-909 stereo microphone. Males generally ceased calling when they were approached (*Gastrophryne* and *Pternohyla* were easily disturbed); only if the observer remained relatively motionless would apparently normal calling behavior be resumed. Release calls were recorded either in the field or in the laboratory by gently compressing the sides of a male held between thumb and forefinger directly above a microphone (following Sullivan 1992). Only slight pressure was necessary to elicit a series of release calls. Cloacal temperatures were measured with a Weber quick-recording thermometer within 5 sec of recording the final advertisement call or release call. Water and air temperatures were generally within 3°C of cloacal temperatures during field recordings.

Acoustic Analysis

Advertisement calls were digitized with a DATA Precision model 610 plug-in digitizer at a sampling rate of 10 kHz (Nyquist frequency = 5 kHz) and analyzed with a DATA Precision 6000 waveform analyzer. Release calls were digitized at a capture rate of 22 kHz on a Macintosh LC computer using a Farallon Corporation MacRecorder and analyzed with SoundEdit software (version 2.03). Call durations were measured to the nearest 0.01 sec with the Waveform analyzer (<2 sec) or with a stopwatch. Pulse rates of advertisement calls were measured over a 0.5-sec interval spanning the call midpoint; all pulses were counted to determine the pulse rate of release calls using the oscilloscope mode of SoundEdit. Dominant frequencies were estimated to the nearest 10 Hz over a 0.25-sec interval spanning call midpoints using the waveform analyzer. Neither advertisement nor release calls are frequency modulated to any large extent in any of the 3 anurans under study. For each male used in analysis of advertisement and release calls, mean values were generated for each of the 3 call variables from 3 or more calls.

Historic Distributions

We obtained specimen listings from the following institutions: American Museum of Natural History (AMNH), Arizona State University (ASU), Brigham Young University (BYU), California Academy of Sciences (CAS), Carnegie Museum of Natural History (CMNH), Los Angeles County Museum (LACM), Museum of Vertebrate Zoology (MVZ), University of Arizona (UA), University of Michigan Museum of Zoology (UMMZ), University of New Mexico (UNM), and United States National Museum (USNM). It is important to note that we examined only specimens deposited in the ASU collection and a portion of those housed at the USNM. We assume that anurans listed by the other institutions are correctly identified. Given that these 3 anurans are quite distinct from other Sonoran Desert forms and therefore unlikely to be misidentified, it seems reasonable to accept these listings in lieu of a physical examination of all specimens. We did, however, obtain detailed information from collectors for any specimen collected outside or on the periphery of the range (e.g., San Xavier region).

RESULTS AND DISCUSSION

Bufo retiformis

Relative to other toads (genus *Bufo*) found in south central Arizona, *B. retiformis* possesses an unusually high-pitched, short-duration advertisement call, often described as an "insect-like buzz" (see Stebbins 1985, Hulse 1978). However, given similarities in advertisement calls of *B. retiformis* and *G. olivacea*, identification based on calls can only be confidently determined with analysis of signals in the laboratory (Sullivan unpublished data). On average, *B. retiformis* calls are longer (μ = 3.0 sec, range = 2.0–4.3 sec at approximately 26° C body temperature) and lower in frequency (μ = 3112 Hz) than calls of *Gastrophryne* (typically 1–2 sec duration at ≈4000 Hz).

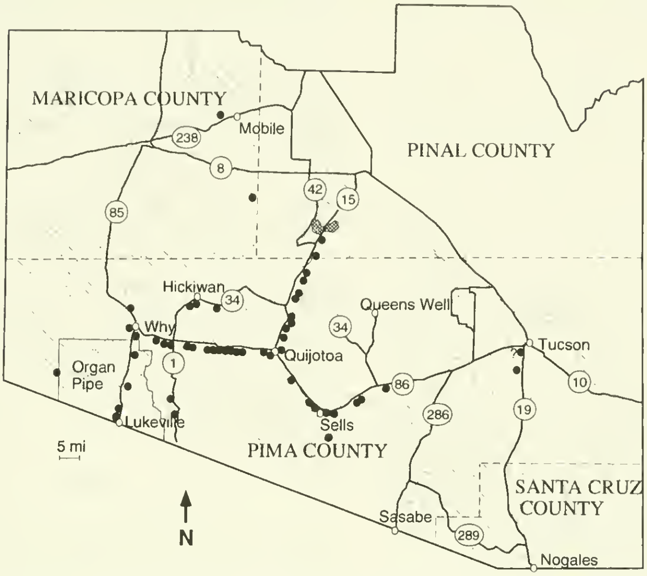
HISTORIC DISTRIBUTION.—*Bufo retiformis* is known from west central Sonora and south central Arizona (Hulse 1978; Fig. 1). Since it was described in 1951, this anuran has been observed in Arizona at sites ranging from near San Cristobal Wash, just west of Organ Pipe Cactus National Monument, north to tributaries of Waterman Wash near Mobile, southeast to the vicinity of Tucson (San Xavier Mission), and southwest to the international border near Sasabe. Across this region it occurs in creosote flats, upland saguaro–palo verde associations, and relatively high-elevation (>900 m) desert grassland.

One historic locality deserves special discussion: southern Vekol Valley, Pinal County. At this site Jones et al. (1983) reported both *B. retiformis* and *B. debilis*. We have examined the single voucher specimens for *B. retiformis* (USNM 252797) and *B. debilis* (USNM 252776; SVL = 43 mm, reproductive female) and determined by comparison with juveniles in the ASU collection (ASU 23099-23102) that the putative *B. debilis* is not simply a juvenile *B. retiformis*. Using the morphometric methods proposed by Ferguson and Lowe (1969), we scored this individual close to *B. debilis* in all respects; hence, the *B. debilis* individual cannot be dismissed as a simple misidentification or hybrid. The presence of *B. debilis* well within the range of *B. retiformis* is especially problematic. No *B. debilis* have been recorded from appropriate habitat spanning the 240 km between Vekol Valley and the otherwise westernmost previous locality for this eastern relative of *B. retiformis* (near Benson, Arizona). Unfortunately, we were unable to survey Vekol Valley when conditions were suitable for anuran activity.

PRESENT DISTRIBUTION.—In 1993–94, we observed *B. retiformis* at or near most historic localities, except San Xavier and Vekol Valley, and at additional sites (Fig. 1). They were especially abundant along Indian Route (IR) 15, 0–40 km north of Quijotoa, associated with the Santa Rosa Wash floodplain. Surveys in which every anuran was identified along a roadway segment (1–65 km) revealed that *B. retiformis* constituted up to 63% of all anurans sighted on this route (Table 1), whereas they were absent or composed a small proportion (<1%) of total anurans sighted on roadways on the periphery of their distribution near Mobile and Sasabe (Table 1). Similarly, this toad was not abundant along State Route (SR) 85 near Organ Pipe Cactus National Monument. During 1993 and 1994 we never observed this species on SR 85 or SR 86 in this westernmost portion of the range. Philip Rosen (personal communication) has observed only a few *B. retiformis* near the international border, and a number of individuals near Why, Arizona, during the course of extensive fieldwork near Organ Pipe Cactus National Monument over the past 6 yr.

Contrary to the suggestion of Hulse (1978; see also Nickerson and Mays 1968), *Bufo retiformis* does not appear to be expanding its range northward into areas of agricultural activity (e.g., southern Pinal County). We conducted many surveys in southern Pinal County: south of Stanfield and south of Arizona City, 2 areas directly north of known localities for *B. retiformis* (Fig 1). We also extensively surveyed the Avra Valley region, Pima County, immediately west of Tucson, and the vicinity of Mobile, Maricopa County. These habitats are similar to areas inhabited by *B. retiformis* directly to the south or west, except that agricultural activity is relatively higher in these areas. It appears that *B. retiformis* is less common on the periphery of its range: near Organ Pipe Cactus National Monument in the west, near Mobile in the north, and in Altar Valley in the east.

a) Historic collecting localities for *Bufo retiformis* in south central Arizona.


MARICOPA COUNTY
PINAL COUNTY
PIMA COUNTY
SANTA CRUZ COUNTY
Mobile
Hickiwan
Why
Organ Pipe
Lukeville
Quijotoa
Queens Well
Tucson
Sells
Sasabe
Nogales
238
8
85
42
15
34
34
1
86
286
19
10
289
5 mi
N

b) Recent collecting localities for *Bufo retiformis* in south central Arizona.

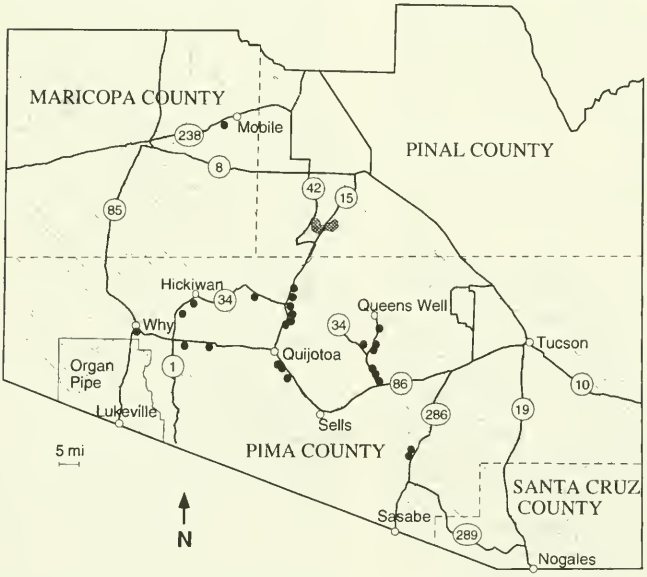

MARICOPA COUNTY
PINAL COUNTY
PIMA COUNTY
SANTA CRUZ COUNTY
Mobile
Hickiwan
Why
Organ Pipe
Lukeville
Quijotoa
Queens Well
Tucson
Sells
Sasabe
Nogales
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Fig. 1. Map of a) historic distribution (•) and b) present distribution (•) of *Bufo retiformis* in south central Arizona.

BREEDING ACTIVITY.—Like many explosive breeding desert anurans, *B. retiformis* will take advantage of a variety of water sources for reproduction. We observed chorusing activity in cattle tanks and roadside pools associated with washes. We observed *B. retiformis* breeding in the same pool with all other explosive breeding anurans that occur in south central Arizona: *B. alvarius, B. cognatus, B. punctatus, Gastrophryne olivacea, Pternohyla fodiens, Scaphiopus couchii*, and *Spea multiplicata*. We never observed *B. retiformis* breeding in the absence of other anurans—minimally, *B. cognatus* and *S. couchii* bred sympatrically with *B. retiformis*.

Male *B. retiformis* typically call positioned beneath vegetation (e.g., small shrubs or grass),

TABLE 1. Numbers of anurans individually identified on road surface over a specified distance. Bal = *B. alvarius*, Bco = *B. cognatus*, Bpu = *B. punctatus*, Bre = *B. retiformis*, Sco = *Scaphiopus couchii*, IR = Indian Route, SR = State Route, MM = mile marker.

Date	Location (approximate)	Survey distance (km)	Species					Total
			Bal (%)	Bco (%)	Bpu (%)	Bre (%)	Sco (%)	
7/18/94	SR 286	40	31 (33)	13 (14)	—	—	49 (53)	93
7/28/94	Arizona City	24	4 (40)	2 (20)	—	—	4 (40)	10
7/29/94	SR 286	72	13 (18)	13 (18)	5 (7)	—	39 (56)	70
8/7/94	Mobile	25	5 (18)	—	3 (11)	1 (3)	19 (68)	28
8/8/94	SR 286	24	3 (23)	4 (31)	—	—	6 (46)	13
8/8/94	Mobile	30	10 (14)	4 (6)	5 (7)	—	51 (73)	70
8/13/94	IR 15, MM 11	4.8	1 (3)	1 (3)	1 (3)	9 (28)	20 (63)	32
8/15/94	IR 15, MM 11	3.4	2 (25)	—	—	5 (63)	1 (13)	8
9/10/94	Stanfield	5.3	64 (75)	9 (10)	1 (1)	—	11 (13)	85

1–5 m from the water's edge. Amplexus is initiated on land with the typically larger female carrying the male to water for oviposition. In high-density aggregations, satellite males can be common—we saw as many as 3 non-calling males near 1 calling male.

Chorusing males and amplexing pairs were observed on only 4 occasions. Three breeding aggregations along IR 15 were relatively large and located at sites used regularly in the past (e.g., 1984, 1986, 1988; Sullivan and Bowker unpublished). At mile marker (MM) 18.7 on IR 15 north of Quijotoa, a large aggregation formed in a shallow roadside pool (8/9/93). Unfortunately, direct counts of all individuals present were not possible due to restricted property access, but complete counts of all males and females along an open section of the pool shoreline (23 calling and satellite males, 5 females in 75 m) allow a rough minimum estimate of >200 males and females for the entire pool (≈600 m circumference). Observations at a 2nd site that same night, a cattle tank (≈25 × 50 m) near MM 8.5, north of Quijotoa, indicate a thriving population in spite of hybridization with *B. punctatus* (see below). On the 1st night (8/9/93) following heavy rainfall in this area, we counted 20 male *B. retiformis* at 0300, calling with numerous *B. alvarius*, *B. cognatus*, and *B. punctatus*. On the following night (8/10/93), approximately 40 male *B. retiformis* were observed, in addition to a minimum of 5 pairs in amplexus. A 3rd breeding aggregation (8/25/94) at a roadside pool (≈50 × 25 m) at MM 11 on IR 15 west of Santa Rosa comprised 19 calling males and 5 amplexing pairs (direct count of all individuals). In contrast to these relatively vigorous aggregations, only 6 males and a single female were observed at a "first-night" chorus (8/20/93) in a large cattle tank (≈25 × 75 m) near Gunsight Wash along SR 85.

HYBRIDIZATION WITH *BUFO PUNCTATUS*.—Bowker and Sullivan (1991) documented a naturally occurring hybrid between *B. retiformis* and *B. punctatus*, and we observed 3 additional hybrids during our investigation (all in August 1993). These hybrids were observed along IR 15, 10–20 km north of Quijotoa. Hybrids are intermediate to the 2 parental forms and unlikely to be confused with any other anurans in the vicinity. Given the apparent rareness of hybrids, it is unlikely that they present a significant concern for the population status of either parental form.

Hybridization between *B. punctatus* and *B. retiformis* is somewhat surprising given dramatic differences in their advertisement calls and habitat preferences (Ferguson and Lowe 1969). Three factors may facilitate hybridization between *B. punctatus* and *B. retiformis* along IR 15 north of Quijotoa. First, along IR 15 we observed relatively high numbers of *B. retiformis* compared to *B. punctatus*, and we also noted satellite males near calling males in these aggregations. Male mating tactics such as active searching and satellite behavior can increase the probability of heterospecific crosses since these tactics subvert active choice by females. Second, although *B. retiformis* is typically found in desert flats and *B. punctatus* generally occurs in rockier, upland regions, the "hybrid zone" along IR 15 (MM 6–12) represents a transition between lowland (Lower Colorado River Subdivision) and upland (Arizona Upland Subdivision) desert habitats that would allow coexistence of both species. Third, habitat modification at the site, namely, road construction and development of cattle tanks, may overcome ecological separation between the species and provide opportunities for hybridization.

Gastrophryne olivacea

As noted above, the advertisement call of *G. olivacea* can be confused with *B. retiformis*. In the hand, this small, narrow-mouthed toad cannot be confused with any other species found in Arizona (Nelson 1972a, 1972b, 1973, Stebbins 1985). Identification based on calls (insect-like buzz) alone must be corroborated by laboratory acoustic analysis.

Although Lowe (1964) listed *G. carolinensis* from the mountains near Nogales, Arizona, Nelson (1972a, 1972b) showed that these individuals do not differ significantly from nearby populations of *G. olivacea* from lower-elevation sites. Having examined specimens from throughout the range in Arizona, we concur with Nelson that only a single taxon occurs north of the international boundary.

HISTORIC DISTRIBUTION.—The range of *G. olivacea* largely overlaps that of *B. retiformis* (Fig. 2), except in Santa Cruz County (e.g., near Pena Blanca) where *Gastrophryne* occurs farther east. Of the 3 anurans surveyed, this species occurs in the widest variety of habitats in Arizona, ranging from low-elevation creosote flats through grasslands to oak-woodland communities near Ruby, Arizona (>1200 m).

Wake (1961) reported calling *G. olivacea* 4.8 km southeast of Ajo. Because no individuals were visually confirmed and because of the difficulty of identifying this species by call, we are inclined to discount the record.

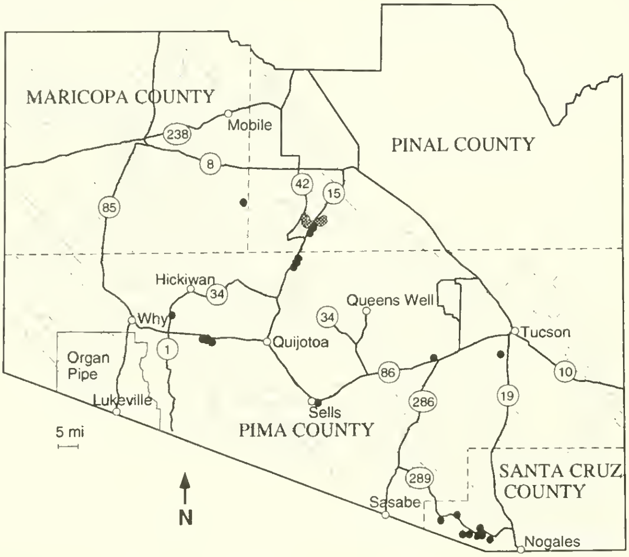
PRESENT DISTRIBUTION.—In 1993–94 we observed *G. olivacea* at most historic localities except those on the eastern margin of the study area (San Xavier and vicinity of Pena Blanca), and at some new sites (Fig. 2). We observed a small chorus near Lukeville, just north of the international boundary, a site that extends the range of *Gastrophryne* approximately 58 km southwest of the previous westernmost locality (San Simon Wash, SR 86) in the United States. Philip Rosen (personal communication) suggests that *Gastrophryne* is more abundant in Mexico to the south and southeast of Lukeville. The absence of previous distributional records from Organ Pipe Cactus National Monument substantiates the notion that *G. olivacea* reaches its northwestern range limit in this area.

We were unable to document *G. olivacea* anywhere along SR 286 (Altar Valley, Buenos Aires Refuge) in spite of apparently adequate habitat and the presence of *G. olivacea* to the east. Philip Rosen (1994 personal communication) observed a number of *G. olivacea* breeding choruses in southwestern Santa Cruz County, just east of the Buenos Aires Refuge boundary, during summer 1994. Hence, this species likely occurs in the area but, like *B. retiformis*, may be less abundant along SR 286. We did not find *G. olivacea* in the vicinity of San Xavier Mission or along SR 289, although we visited these sites after rainfall on several occasions. Our failure to document *Gastrophryne* in areas with appropriate habitat may be an artifact of its secretive habits (i.e., individuals may not come on road surfaces) and small size (i.e., they are difficult to detect when on a road).

BREEDING ACTIVITY.—*Gastrophryne olivacea* are usually well concealed in vegetation when calling and possess a call that is extremely difficult to localize. They call next to water sources or from floating vegetation. Male satellite activity was not observed. Although *G. olivacea* has been observed in choruses with all other sympatrically breeding anurans (see above listing under *B. retiformis*), on many occasions we observed it in large, relatively monotypic aggregations (e.g., MM 26.7 and 35, IR 15). In these areas *Gastrophryne* often breeds in dense stands of mesquite shrubs growing in the floodplain of Santa Rosa Wash.

Choruses of *Gastrophryne* are easily detected, and we were led to a number of new *Gastrophryne* localities by their distinctive vocalizations. Because of their secretive nature, we never observed pairs in amplexus, and thus no definitive estimates of population size were obtained for breeding choruses of *G. olivacea*.

a) Historic collecting localities for *Gastrophryne olivacea* in south central Arizona.


MARICOPA COUNTY
Mobile
238
8
PINAL COUNTY
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15
85
Hickiwan
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Queens Well
34
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Tucson
Organ Pipe
1
Quijotoa
86
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Lukeville
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Sells
PIMA COUNTY
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SANTA CRUZ COUNTY
289
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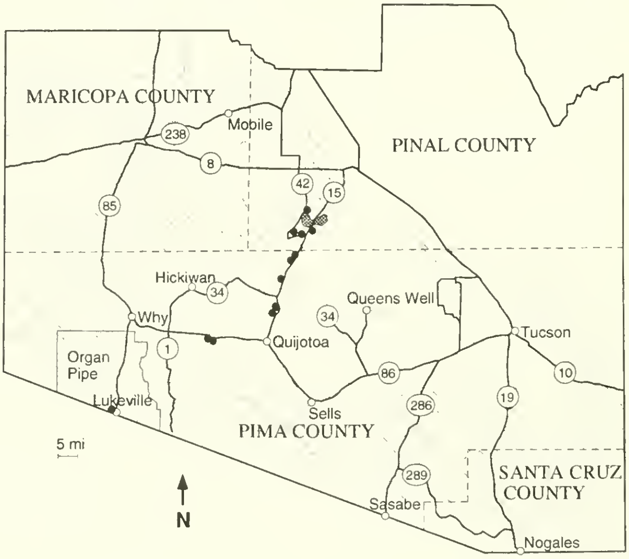
Nogales

b) Recent collecting localities for *Gastrophryne olivacea* in south central Arizona.


MARICOPA COUNTY
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Quijotoa
86
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Lukeville
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Sells
PIMA COUNTY
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SANTA CRUZ COUNTY
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Nogales

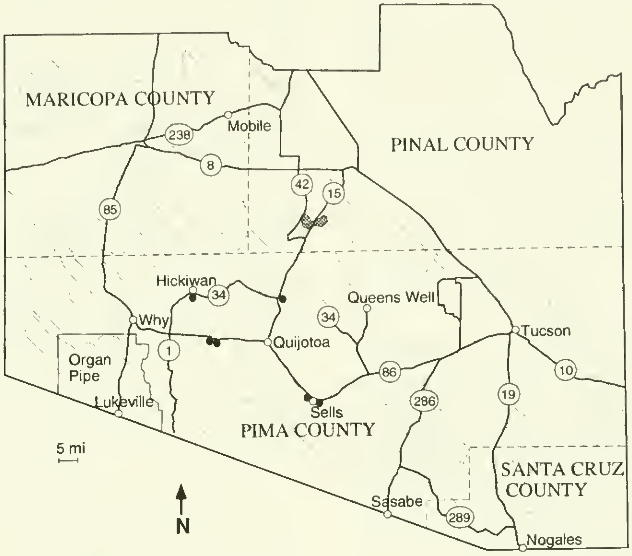
Fig. 2. Map of a) historic distribution (•) and b) present distribution (•) of *Gastrophryne olivacea* in south central Arizona.

By walking the perimeter of rain-formed pools, we obtained rough estimates of >200 calling males at 2 sites along IR 15, 43 and 56 km north of Quijotoa, respectively, on recent (8/9/93) and previous surveys (1984; Sullivan and Bowker unpublished). Unfortunately, since these pools contained considerable vegetation (mesquite shrubs, grass), chorus sizes can only be considered approximate (individual toads were not visually verified). By contrast, at Lukeville (8/9/94) only 5 calling males were present in a small pool (5 × 10 × 0.25 m). Rain had fallen the previous 2 nights (8/7–8/8), and several small egg masses were observed.

Pternohyla fodiens

The advertisement call of *Pternohyla fodiens* is a distinctive "wonk" repeated at a relatively high rate (2/sec: "wonk-wonk-wonk . . . ," etc; see Trueb 1969). Males also produce a call,

a) **Historic collecting localities for *Pternohyla fodiens* in south central Arizona.**


MARICOPA COUNTY
PINAL COUNTY
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Hickiwan
Queens Well
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Quijotoa
Tucson
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Lukeville
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Sasabe
Nogales
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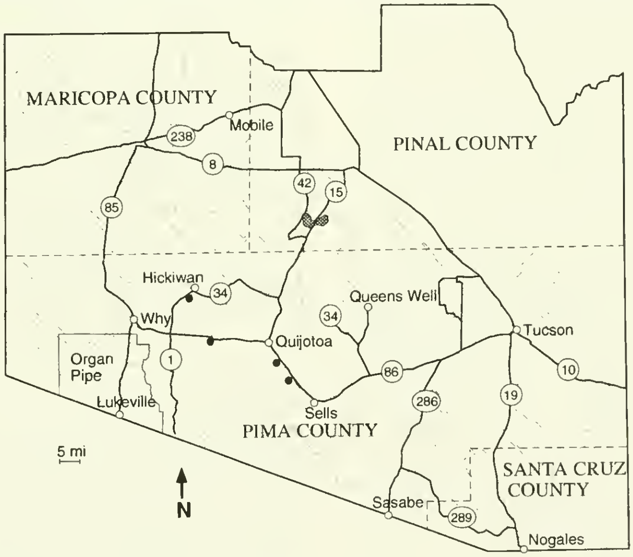
b) **Recent collecting localities for *Pternohyla fodiens* in south central Arizona.**


MARICOPA COUNTY
PINAL COUNTY
PIMA COUNTY
SANTA CRUZ COUNTY
Mobile
Hickiwan
Queens Well
Why
Quijotoa
Tucson
Organ Pipe
Lukeville
Sells
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Nogales
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Fig. 3. Map of a) historic distribution (•) and b) present distribution (•) of *Pternohyla fodiens* in south central Arizona.

which, based on similarities with other hylids, can be tentatively classified as a territorial call. This putative territorial call sounds much like the advertisement call of *Pseudacris triseriata* or the sound of a finger sliding across a comb.

HISTORIC DISTRIBUTION.—This anuran has been observed at a few sites (Fig. 3). All localities but Santa Rosa Wash are associated with washes that flow south toward Mexico: San Simon Wash, and its 2 largest tributaries, Hickiwan and Sells washes. Randy Babb (personal communication) has heard the distinctive vocalization of *Pternohyla fodiens* many times and visually identified at least 1 individual approximately 16 km north of Quijotoa, west of IR 15, in the floodplain of Santa Rosa Wash.

PRESENT DISTRIBUTION.—In 1993–94 we observed *P. fodiens* at most historic localities except Santa Rosa Wash and the vicinity of Sells, and at some additional sites (Fig. 3).

More than the other target species, *P. fodiens* is found in association with washes. The 2 new localities we documented are both associated with small tributaries of Sells Wash, a tributary of San Simon Wash.

During the preparation of this report, Thomas R. Jones and Ross J. Timmons (personal communication) found a single male *P. fodiens* near Santa Rosa Wash, 1 km north of the Pinal County line and west of IR 15 (12 July 1995). This record confirms the presence of *P. fodiens* in Santa Rosa Wash, well north of the San Simon Wash system.

Pternohyla fodiens is only rarely found on road surfaces, although specimens can be taken near washes when roads are wet (e.g., SR 86 at San Simon Wash). Similar to *Gastrophryne*, *Pternohyla* can be easily missed unless chorus activity is underway when a survey is conducted. Because of their extremely explosive breeding habits and the lack of sufficient rainfall near Sells during the survey period, it is not surprising that we observed no *Pternohyla* at the historic localities along Sells Wash near SR 86.

BREEDING ACTIVITY.—We observed breeding aggregations of *Pternohyla fodiens* only in rain-formed pools associated with washes. Calling males are always in or near water, and of the 3 survey anurans *Pternohyla* seems more dependent on heavy rainfall to initiate breeding activity. This species appears to exhibit the most explosive mating system of the 3 species. We never observed *Pternohyla* chorusing more than 36 h after rainfall; by contrast, both *Gastrophryne* and *Bufo* were observed in chorus activity 1–4 nights following rainfall.

The only significant *Pternohyla* chorusing that we observed occurred near Hickiwan (7/13/93) and San Simon Wash (7/13/93). Although direct counts were not possible, estimates from chorusing intensities suggest that dozens, if not hundreds, of calling males may have been present at San Simon Wash along SR 86; however, only a single pair in amplexus was observed. Large aggregations of *Pternohyla* have been observed at these sites regularly over the past 30 yr (Sullivan and Bowker unpublished).

SUMMARY

Our survey indicates that all 3 target species are present at most historic localities in south central Arizona. We documented range extensions to the northwest and southeast for *B. retiformis* (Mobile/SR 286) and to the southwest for *Gastrophryne olivacea* (Lukeville). These forms probably occur at all historic localities, since our inability to verify their presence at some sites undoubtedly resulted from the absence of sufficient rainfall. It is critical to note that our survey methods, although allowing rapid coverage of a relatively large area, were limited by unpredictable rainfall and the secretive nature of the target species (especially *Pternohyla* and *Gastrophryne*). Unless chorusing activity was underway when we visited an area, the presence of any of the 3 forms may have been overlooked. In the absence of chorusing activity, *Bufo retiformis* was the only target species regularly found on road surfaces.

Minimally, the presence of these anurans at most historic localities suggests no widespread decline as experienced by other anuran amphibians in the United States (e.g., ranid frogs of the Southwest; Michael Sredl personal communication). Future work should address estimation of population levels through mark-recapture methods in conjunction with intensive monitoring of single sites throughout as many consecutive activity periods (June–September) as possible. An understanding of factors contributing to variations in species abundance will require long-term study.

ACKNOWLEDGMENTS

This research was supported by an IIPAM award (192004) from the Arizona Game and Fish Department Heritage Fund. We gratefully acknowledge the assistance of the Tohono O'Odham Nation, especially the Department of Public Safety personnel. In addition, Henry Ramon of the Hickiwan District, Norbert Manuel of the Sells District, and Madeline Sakiestewa and Jefford Francisco of the Baboquivari District were especially helpful in coordinating activities. Mike Demlong, Robert Dudley, Matthew Goode, Matthew Flowers, and Michael Sredl provided assistance with field observations. Randy Babb, Darrel Frost, Jeff Howland, K. Bruce Jones, Thomas R. Jones, Clayton May, Phil Rosen, Cecil Schwalbe, Norm Scott, and Michael Sredl graciously shared their field records and experiences.

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APPENDIX 1

Specimen numbers for historic collecting localities for *Bufo retiformis*, *Gastrophryne olivacea*, and *Pternohyla fodiens*. Institutional abbreviations: AMNH = American Museum of Natural History, ASU = Arizona State University vertebrate collection, BYU = Brigham Young University collection, CAS = California Academy of Sciences, CMNH = Carnegie Museum of Natural History, LACM = Los Angeles County Museum, MVZ = Museum of Vertebrate Zoology, UAZ = University of Arizona, UMMZ = University of Michigan Museum of Zoology, UNM = University of New Mexico, USNM = United States National Museum.

Bufo retiformis: AMNH 59189, 60671, 85357-65, 91953-54, 102234-36; ASU 3298-3300, 3894-3902, 3942-48, 8002, 8004, 8005, 22775-76, 23099-102, 23252, 24038-39, 24273-74, 25552-53; BYU 42119; CAS 91501-04, 94390-95, 98055-56, 188354-55; CMNH 51562, 53841-42, 53855, 63520, 89782-95; LACM 26086-88, 64180-84, 88380-400, 91833, 105719, 115266-314, 123234-41, 137788-89; MVZ 71906-07, 73751-52, 74206-32, 76620-28, 81269, 139130, 180219-22, 180358-59; UAZ 12369-75, 14848-49, 25847-48, 31381, 43011; UMMZ 133460, 136395, 134077; UNM 30993-995, 31268, 40207, 41686-87; USNM 226443-45, 245988, 252797, 322966.

Gastrophryne olivacea: AMNH 88986, 91971-80, 119746; ASU 14014, 22059-60, 22224-25, 22969-70, 22771-74, 23095, 23411, 24259-60, 25664-66; CMNH 63138-39; LACM 26576-81, 91896, 115511, 112480, 123293; MVZ 49479-504, 58922, 72304-05; UAZ 26993-96, 29101-04, 29107, 42187-91, 38181, 35163-64, 38179, 38200-01, 38180, 38197-99, 29027; USNM 252817; UMMZ 136400, 75737-38, 75753, 92300.

Pternohyla fodiens: AMNH 91964-70, 95147; ASU 3301, 13952-68, 22777-80, 24276, 25556-61; CAS 91505; CMNH 63188-89; LACM 90170-82, 115447-75; MVZ 71905, 73747-48, 80104-21, 81271, 178447, 76629-33; UNM 40201, 40204.

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HABITAT AFFINITIES OF BATS FROM NORTHEASTERN NEVADA

Mark A. Ports[1] and Peter V. Bradley[2]

ABSTRACT.—Bat surveys were completed in 6 habitat types in eastern Nevada between 1980 and 1994. Twelve species of bats and 578 individuals were identified from 33 trap localities in 144 trap nights. There were weak correlations between bat species richness and January maximum temperatures (0.728, $P < 0.05$) and mean annual days with 0° C or lower (−0.704, $P < 0.05$). Bat species richness exhibited no correlation with annual normal precipitation, January minimum temperatures, July minimum temperatures, and July maximum temperatures. It appears that bat species richness is highest in portions of northeastern Nevada typified by sedimentary deposits (limestone, dolomite). Igneous mountain ranges (basalt, volcanic ash) generally had moderate bat species richness, and metamorphic mountain ranges (quartzite) typically had low bat species richness. Notable range extensions include *Antrozous pallidus* (from central Nye County north to the Nevada-Idaho border, approximately 450 km), *Tadarida brasiliensis* (approximately 350 km north), and *Pipistrellus hesperus* (approximately 350 km north). Also, the presence of *Lasionycteris noctivagans*, *Lasiurus cinereus*, and *Corynorhinus townsendii* was confirmed.

Key words: bats, Chiroptera, Nevada, habitat.

Although the distribution of mammals of the Great Basin has been studied in some detail (Hall 1946, Durrant 1952, Brown 1971, Thompson and Mead 1982, Wells 1983, Grayson 1987), bats remain poorly known. There are very few recent records of bats from the northern Great Basin of Oregon, Idaho, and Nevada (Hall 1946, Durrant 1952, Larrison and Johnson 1981). Here we present new information on habitat affinities and distribution of 12 species of bats from eastern and northeastern Nevada. Such information may prove valuable to land managers and wildlife biologists who make decisions on how to deal with the impact of human activities on bats.

METHODS

Study Area

Northeastern Nevada is part of the Great Basin Division of the Intermountain Floristic Region (Holmgren 1972), an area of continental climate with fairly hot summers and cold, snowy winters. Some 30 north/south-trending fault-block mountain ranges (3000–4000 m) are separated by high-elevation (1500–2000 m) xeric basins.

Mountain ranges in northern Elko, Eureka, Humboldt, and Lander counties are mostly igneous and metamorphic fault blocks, covered with various mountain brush communities and fragmented coniferous and deciduous forests. Perennial streams produce riparian habitats in most canyons. Vertical cliffs and stands of deciduous and coniferous trees provide sites for day roosting and shelter for maternity activities. Valley floors are mostly xeric, covered with salt-tolerant shrubs (*Atriplex* spp., *Sarcobatus* spp.) and sagebrush (*Artemisia* spp.). Occasional perennial streams extend onto valley floors and are lined with narrow corridors of deciduous woodlands and mesic shrubs.

Mountain ranges in eastern Nevada (White Pine and southern Eureka and Lander counties) are predominantly limestone and dolomite fault blocks and tend to have more xeric plant communities. A large number of natural caves and vertical cliff sites provide excellent habitats for bat maternity and hibernation roosts. Natural perennial springs found near the valley/mountain fault lines often provide the only dependable water for miles around. Contiguous coniferous forests on some of the higher mountain slopes provide suitable tree roosts. Abandoned mine shafts and adits are abundant in northeastern Nevada and are critically important to some bat species, both summer and winter.

Survey Methods

Surveys began in the summer of 1980 and extended through the fall of 1994. Capture

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methods included mist nets, hand capture, and harp trap (Kunz and Kurta 1990). Mist nets and the harp trap were used over perennial streams, small springs, beaver ponds, livestock tanks, in forest canopies, and adjacent to mine shafts, adits, and natural caves. Captured bats were identified, sexed, reproductive status recorded, aged, weighed, and then released. Some individuals were taken as voucher specimens and are temporarily held in the vertebrate collection of Great Basin College. S. Altenbach (personal communication) and M. O'Farrell (personal communication) assisted in identifications. Localities were identified on 1:100,000 scale metric topographic maps.

To describe habitat affinities, we delineated 6 general habitat types for the region: C–river **canyons** in igneous or metamorphic rock, above low-gradient, perennial streams lined with cottonwood (*Populus* spp.), willow (*Salix* spp.), and mesic shrubs (*Rosa* spp. and *Ribes* spp.), elevation approximately 2200 m; **S**–foothill and valley **springs**, with or without deciduous trees and a surrounding area of salt-tolerant shrubs (*Atriplex* spp., *Sarcobatus* spp.) or mountain brush (*Artemisia* spp., *Amelanchier* spp., *Sambucus* spp., *Symphoricarpos occidentalis, Purshia tridentata*) communities, elevation approximately 2000 m; **F**–mid- to high-elevation coniferous **forests** of juniper (*Juniperus osteosperma*), fir (*Abies concolor* and *A. lasiocarpa*), spruce (*Picea engelmannii*), and pine (*Pinus monophylla, P. flexilis,* and *P. longaeva*) often with cliff sites and natural caves in the proximity, elevation approximately 2300–3000 m; **D**–mid- to high-elevation **deciduous** forests of aspen (*Populus tremuloides*), cottonwood (*Populus* spp.), and mesic shrubs (*Amelanchier* spp., *Prunus* spp., *Betula occidentalis, Alnus tenuifolia*) often along high-gradient, perennial streams, elevation approximately 2300–2800 m; **U**–natural caves and **underground** mine shafts/adits with surrounding plant communities described in habitats C, F, S, and D; and **B–buildings** in towns and on ranches. There may also be additional important bat habitats not yet identified in this region.

RESULTS AND DISCUSSION

A total of 578 individuals of 12 species of bats were identified from 33 trap localities in 144 trap nights from eastern and northeastern Nevada (Tables 1, 2 and Appendix 1). Three species of *Myotis*, (*M. evotis, M. volans,* and *M. ciliolabrum*) were the most widespread (Appendix 1) and had the highest occurrence (Tables 1, 2) of bats from eastern Nevada. *M. evotis* was one of the most abundant species of *Myotis* in eastern Nevada and occurred in all habitats except towns and around buildings. This species is most often associated with mid-elevation pinyon pine and Utah juniper woodlands (Manning and Jones 1989). We, too, found this species to be most abundant in this habitat type (localities 8, 9, and 18, Table 1). *M. evotis* depended heavily on the presence of natural springs within these woodlands as their sole source of water. *M. volans* was also found to utilize a variety of habitats in eastern Nevada, including pinyon-juniper woodlands such as those found near Old Man's Cave. Eight lactating females were examined at this site, suggesting a nearby nursery colony. Upon release, 4 individuals flew into the cave while the others flew to nearby rock outcrops. The literature suggests that this species uses cracks in cliff sites and areas beneath bark as roost sites and caves only as hibernacula (Warner and Czaplewski 1984). It is possible that *M. volans* is using caves in eastern Nevada as maternity roosts, although more data are needed to confirm this. *M. ciliolabrum* also occurred in a variety of habitats in eastern Nevada (Table 1), including river canyons with surrounding sagebrush deserts (locality 14, Appendix 1). Larrison and Johnson (1981) found this species in similar canyon and desert habitat in central Idaho.

Only 6 individuals of *M. lucifugus* were caught. This species was uncommon and more restricted in its habitat affinities. Unidentified specimens of *Myotis* were sent to Dr. Scott Altenbach and Dr. Mike O'Farrell to determine whether or not *M. californicus* is present in this region (Table 2, *Myotis* spp.). Tentative identifications suggest that *M. californicus* may be found in southern White Pine County, while *M. ciliolabrum* is more common in the remainder of the region.

The 3 high-elevation, tree-roosting species (*L. noctivagans, E. fuscus,* and *L. cinereus*) were found in order of decreasing occurrence (Table 1). These species were found repeatedly in several mountain ranges of eastern Nevada that have a combination of coniferous and/or deciduous trees (aspen, cottonwood, white fir, subalpine fir, and Engelmann spruce) for

TABLE 1. Occurrence of bat species by locality (see Appendix 1). Habitat affinities (C–river canyons, S–springs, F–high-elevation coniferous forests, D–mid-elevation deciduous forests, U–underground caves and mines, B–buildings) for each species and relative frequencies for each species examined.

Bat species	Localities (Appendix 1)	Habitat affinities
Myotis ciliolabrum	2, 6, 8, 9, 10, 11, 12,14, 17, 20, 25, 26, 29, 32, 33	C, S, F, D, U, B
Myotis evotis	1, 3, 4, 6, 8, 9, 11, 12, 15–19, 21, 22, 25, 32, 33	C, S, F, D, U
Myotis lucifugus	5, 12, 15–17	C, F, D, U
Myotis volans	1, 2, 6, 7, 9–12, 15, 17–19, 24, 25, 27, 32	C, S, F, D, U
Lasiurus cinereus	10, 17, 20	S, F, D
Lasionycteris noctivagans	10–12, 17, 23, 28, 29, 32	C, S, F, D, B
Eptesicus fuscus	10, 12, 17, 23, 26, 29, 32	C, S, F, D, U, B
Pipistrellus hesperus	10, 29	S, B
Corynorhinus townsendii	5, 9, 10, 13–15, 24–27, 30, 32	C, S, U
Antrozous pallidus	10, 14, 15, 25	C, S, U
Tadarida brasiliensis	10, 29, 31, 32	S, U, B

roosting and open water in the form of beaver ponds, stock tanks, and perennial streams for foraging and drinking sites. In the mountains of the West, these 3 species are known to commonly forage together in similar habitats along with 2–4 species of *Myotis* (Kunz 1982). In eastern Nevada high-elevation deciduous and coniferous forests are limited to watered drainages and north-facing slopes in the larger mountain ranges. This suggests that these species are uncommon when compared to populations in the northern Rocky Mountains and may be negatively impacted by deterioration, fragmentation, and/or total removal of forest habitats by hard-rock mining, livestock grazing, and logging.

Foothills covered with pinyon pine and Utah juniper, caves, and river canyons with high cliffs provided habitats for 2 lower-elevation breeding species, *Corynorhinus townsendii* and *A. pallidus*. *C. townsendii* had 4 times the frequency of occurrence as *A. pallidus* and appeared to be more evenly distributed across the region (Table 1). *C. townsendii* and *A. pallidus* depend heavily on cliff sites, natural caves, and mine shafts/adits for maternity, hibernation, and day roosts in eastern Nevada. They are found to utilize similar situations in other arid regions of the West, such as California, Montana, Washington, and Utah (Kunz and Martin 1982). Hermanson and O'Shea (1983) rarely found *A. pallidus* using caves, but rather found them depending heavily on crevices and cliff sites for maternity roosts, day roosts, and hibernacula. We found this species using caves (localities 15, 25), cliff sites (14), and valley springs (10) in eastern Nevada.

A large, historic colony of *T. brasiliensis* was found occupied in July 1994. Vandalism may have caused this population to roost elsewhere in 1992 and 1993. Outside of Las Vegas and Reno, this colony is the largest known concentration of mammals in Nevada. Based on visual techniques suggested by Kunz and Kurta (1990), we estimate the population at between 54,000 and 82,000 animals.

P. hesperus was found in low numbers in this region. Two individuals were caught 320 km apart, and no meaningful habitat patterns were identified for this species.

Species found in and around abandoned mine shafts and adits included *C. townsendii*, *M. ciliolabrum*, and *M. volans*. *C. townsendii* was found using mines during both winter and summer. *Myotis* species were found only in summer. Pat Brown (personal communication) recently documented a maternity colony of *Antrozous pallidus* in an abandoned mine shaft in northern Lander County as well.

Climatological data from Elko in the northeastern part of the state, Ely in the east central, and Las Vegas in the south were compared to

TABLE 2. Number of bats examined, percent frequency by species, and number of specimens collected and preserved from eastern Nevada (1980–1994).

Bat species	Number of bats examined	% frequency	Specimens collected
Myotis ciliolabrum	73	13.0	2
Myotis evotis	112	19.0	3
Myotis lucifugus	6	0.4	1
Myotis volans	186	32.0	3
Myotis spp.	16	3.0	2
Lasiurus cinereus	3	0.1	1
Lasionycteris noctivagans	39	7.0	4
Eptesicus fuscus	52	10.0	2
Pipistrellus hesperus	2	0.1	0
Corynorhinus townsendii	69	12.0	1
Antrozous pallidus	15	3.0	1
Tadarida brasiliensis[a]	5	0.4	2
TOTAL	578	100.0	22

[a] Roost cavern not included in calculations.

bat species richness from each of these regions (Hall 1946, Durrant 1952). Pearson's $\mathfrak{R}$ and Spearman's Rho tests were used to test for correlations. Bat species richness exhibited no correlation with the following climatological data: annual normal precipitation, January minimum temperatures, July minimum temperatures, and July maximum temperatures. There were weak correlations between bat species richness and January maximum temperatures (Pearson's $\mathfrak{R}$, 0.728, $P < 0.05$) and mean annual days with 0° C or lower (Pearson's $\mathfrak{R}$, –0.704, $P < 0.05$).

Bat records were pooled by mountain ranges with similar rock types—sedimentary, igneous, or metamorphic. Bat species richness was highest in portions of northeastern Nevada typified by sedimentary rock (limestone, dolomite). Igneous mountain ranges (basalt, volcanic ash) generally had moderate bat species richness, and metamorphic mountain ranges (quartzite) typically had low bat species richness.

Several bat localities from eastern Nevada represent notable range extensions. Four localities (10, 14, 15 and 25, Appendix 1) for *A. pallidus* extend its range from central Nye County (Hall 1946) north to the Nevada and Idaho border, approximately 450 km. Two specimens of *T. brasiliensis* at Swallow Canyon (locality 10, Appendix 1), the recent confirmation of a large roost colony, and the two specimens from Elko (locality 29, Appendix 1) represent the first records of this species for Elko and White Pine counties (Hall 1946) and extend its range approximately 350 km north. The capture of single specimens of *P. hesperus* at Swallow Canyon (locality 10, Appendix 1) and in Elko (locality 29, Appendix 1) also suggest a northern range extension and, based on spring and late-summer capture dates, may represent migrating individuals.

Although certain bat species have long been suspected of occurring in this region (Hall 1946, Durrant 1952, Kunz 1982, Kunz and Martin 1982), the localities listed in Appendix 1 represent the first range confirmations for *L. noctivagans*, *L. cinereus*, and *C. townsendii* in eastern and northeastern Nevada.

On examination of contributing abiotic factors such as geological features, precipitation, and average temperatures, one can see patterns in eastern Nevada's bat fauna beginning to emerge. The greatest diversity of bat species from eastern Nevada was recorded in east central Nevada. The lower maximum January temperatures and more annual days below 0° C in east central Nevada contradicted the correlations in our data and suggested that factors other than climate were contributing to zoogeographical patterns. East central Nevada's mountain ranges are primarily sedimentary in nature and provide abundant caves, cliff sites, and high-elevation forests for roosting and hibernation. In northeastern Nevada most of the mountain ranges are igneous or metamorphic in structure, thus reducing the number of potential roost sites for bats. Climatic factors undoubtedly play a large role in defining bat distribution. However, the density of suitable roost sites may prove to be an even greater influence on bat distribution where roost site availability becomes a limiting factor. Inasmuch as most bat species probably do not migrate more than 1500 km from maternity roosts to hibernacula (Hill and Smith 1992), an abundance of suitable hibernation roosts would probably provide any given bat fauna the best chance of survival in an area where severe winters are commonplace.

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APPENDIX 1
BAT SURVEY LOCALITIES AND ANIMALS EXAMINED

1. Stump Creek, 8.2 mi S and 7.6 mi W of Northfork, Independence Mountains, Elko Co., Nevada. T40N, R53E, SW1/4 sec 12. 2325 m. 17 July 1980, *Myotis evotis* (1), *M. volans* (2).

2. Sheep Creek, 8.5 mi S and 7.8 mi W of Northfork, Independence Mountains, Elko Co., Nevada. T40N, R53E, NW1/4 sec 13. 2320 m. 6–7 August 1980, *Myotis volans* (1 lactating female), *M. ciliolabrum* (1 male).

3. Jim Creek, 10.4 mi S and 7.2 mi W of Northfork, Independence Mountains, Elko Co., Nevada. T40N, R53E, NE1/4 sec 25. 2155 m. 15 July 1981, *Myotis evotis* (2 nonscrotal males).

4. Jarbidge River, 5.5 mi S and 1.2 mi E of Jarbidge, Jarbidge Mountains, Elko Co., Nevada. T45N, R58E, SE1/4 sec 10. 2460 m. 26 July 1981, *Myotis evotis* (1).

5. Northfork of the Humboldt River, 12.4 mi S and 2.5 mi E of Northfork, Elko Co., Nevada. T39N, R55E, center sec 3. 1850 m. 7 Sept. 1981, *Corynorhinus townsendii* (1); 30 August 1989, *Myotis lucifugus* (1).

6. Mouth of Cave Creek, Ruby Lake National Wildlife Refuge, east slope of the Ruby Mountains, Elko Co., Nevada. T27N, R57E, SW1/4 sec 24. 1850 m. 25 July 1986, *Myotis volans* (2), *M. evotis* (1); 15 June 1987, *Myotis evotis* (1), *M. ciliolabrum* (1).

7. Ferguson Springs, 1/4 mi W of Ferguson Station on St. Hwy 93, Elko Co., Nevada. T30N, R69E, NE1/4 sec 33. 1875 m. 17 Sept. 1989, *Myotis volans* (1).

8. Arizona Springs, southeast end of the East Humboldt Range, Elko Co., Nevada. T33N, R61E, SW1/4 sec 20. 2050 m. 21 June 1991, *Myotis evotis* (9 males, 18 lactating females), *M. ciliolabrum* (3 males).

9. Sidehill Spring, 6.4 mi S and 11.8 mi W of Wendover, Goshute Mountains, Elko Co., Nevada. T32N, R68E, SW1/4 sec 14. 2255 m. 7 June 1991, *Myotis evotis* (6 males, 2 lactating females), *M. volans* (4 males, 2 lactating females), *M. ciliolabrum* (1), *Corynorhinus townsendii*, 1 male.

10. Swallow Canyon, spring site at the mouth of the canyon, Snake Range, White Pine Co., Nevada. T11N, R68E, sec 5. 2100 m. 21 August 1991, *Myotis ciliolabrum* (1), *Lasionycteris noctivagans* (1 male, 2 females), *Lasiurus cinerius* (1 male), *Tadarida brasiliensis* (2 males), *Antrozous pallidus* (1 lactating female); 30 August 1991, *Myotis volans* (1 male), *Lasionycteris noctivagans* (19 males), *Pipistrellus hesperus* (1 male), *Eptesicus fuscus* (2 males), *Corynorhinus townsendii* (1 male); 22 August 1994, *Myotis*

volans (8), *M. evotis* (1), *M. ciliolabrum* (11), *Corynorhinus townsendii* (1), *Lasionycteris noctivagans* (2), *Eptesicus fuscus* (1).

11. Headwaters of McCall Creek, Bull Run Mountains, Elko Co., Nevada. T45N, R52E, middle sec 23. 2420 m. 6 July 1991, *Myotis volans* (2), *M. evotis* (1), *M. ciliolabrum* (1), *Lasionycteris noctivagans* (2).

12. Mary's River, 6.5 mi S and 2 mi W of Mary's River Peak, Jarbidge Mountains, Elko Co., Nevada. T44N, R58E, SW1/4 sec 35. 2220 m. 30 July 1990, *Myotis evotis* (2 males), *M. ciliolabrum* (1 lactating female), *Eptesicus fuscus* (1 lactating female); 31 July 1990, *Myotis lucifugus* (2 males), *M. evotis* (1 lactating female), *M. volans* (1 male, 2 lactating females, 5 nonlactating females), *M. ciliolabrum* (2 females), *Eptesicus fuscus* (1 male, 1 female), *Lasionycteris noctivagans* (2 males); 1 August 1990, *Myotis volans* (2 males, 3 lactating females), *M. evotis* (1 lactating female), *Eptesicus fuscus* (2 males), *Lasionycteris noctivagans* (2 males).

13. Complex of mine shafts in Snowstorm Mountains, canyon 1.5 mi N of Midas, Elko Co., Nevada. T39N, R46E, NW1/4 sec 16. 1950 m. 31 May 1992, *Corynorhinus townsendii* (3).

14. Salmon Falls Creek, 1.6 mi W of Jackpot, Elko Co., Nevada. T47N, R64E, center sec 10. 1500 m. 23 May 1992, *Myotis ciliolabrum* (1); 24 June 1992, *Myotis ciliolabrum* (1), *Antrozous pallidus* (3 males, 1 lactating female), *Corynorhinus townsendii* (1 lactating female).

15. Goshute Cave[3], Cherry Creek Range, White Pine Co., Nevada. T25N, R63E. 20 June 1992, *Myotis evotis* (2), *M. lucifugus* (1), *Corynorhinus townsendii* (3), *Antrozous pallidus* (3); 16 August 1992, *Myotis evotis* (2 males, 4 lactating females), *M. volans* (2 scrotal males), *Myotis* spp. (either *ciliolabrum* or *californicus*) (1 scrotal male), *Antrozous pallidus* (3 scrotal males, 1 nonscrotal male), *Corynorhinus townsendii* (5 scrotal males).

16. Bruneau River, junction of Cottonwood Creek and the Bruneau, Elko Co., Nevada. 1725 m. T45N, R57E, NW1/4 sec 20. 7 June 1992, *Myotis evotis* (1), *M. lucifugus* (1 pregnant female); 22 July 1992, *Myotis evotis* (1).

17. Mill Creek, 1.6 mi N and 2.4 mi W of Jack Creek Campground, Independence Range, Elko Co., Nevada. T42N, R53E, SW1/4 sec 16. 2620 m. 15 July 1992, *Myotis evotis* (1), *M. ciliolabrum* (5 males, 6 lactating females), *M. volans* (1), *M. lucifugus* (1), *Eptesicus fuscus* (3 males, 4 lactating females), *Lasionycteris noctivagans* (3), *Lasiurus cinereus* (1).

18. Water Canyon and Buck Springs, southwest slope of the Ruby Mountains, White Pine Co., Nevada. T25N, R56E, NW1/4 sec 1 and T26N, R56E, center of sec 35, respectively. 2300 m. 6 July 1992, *Myotis evotis* (3 scrotal males, 2 females), *M. volans* (2 scrotal males, 3 females), *M. californicus* (1 scrotal male); 22 July 1993, *Myotis evotis* (17), *M. volans* (2), *M. californicus* (2).

19. Middlefork of Doby George Creek, 1.2 mi S of Maggie Creek Summit, Bull Run Mountains, Elko Co., Nevada. 2050 m. 27 July 1992, *Myotis evotis* (4), *M. volans* (1).

20. Horse Creek, 5.2 mi W and 0.4 mi N of Secret Pass, East Humboldt Range, Elko Co., Nevada. T34N, R61E, NE1/4 sec 16. 2520 m. 4 August 1993, *Myotis ciliolabrum* (7), *Lasiurus cinereus* (1).

21. USFS campground on Northfork of Berry Creek, Schell Creek Range, White Pine Co., Nevada. T17N, R65E, SE1/4 sec 10. 2550 m. 9 July 1993, *Myotis evotis* (3 lactating females).

22. Worthington Canyon, Schell Creek Range, White Pine Co., Nevada. T17N, R65E, center sec 16. 2550 m. 10 July 1993, *Myotis evotis* (3).

23. Currant Creek, USFS campgrounds, 1.8 mi E and 0.8 mi S of Currant Mountain, White Pine Co., Nevada. 2650 m. 11 July 1993, *Eptesicus fuscus* (1), *Lasionycterus noctivagans* (1).

24. Old Man's Cave, North Snake Range, White Pine Co., Nevada. T15N, R70E. 16 August 1993, *Corynorhinus townsendii* (4 scrotal males, 1 nonscrotal male, 4 lactating females, 4 nonlactating females), *Myotis volans* (1 scrotal male, 5 nonscrotal males, 9 females), *Myotis* spp. (2 males, 1 lactating female, 1 nonlactating female); 7 September 1994, *Corynorhinus townsendii* (7 males, 17 females), *Myotis volans* (2 females).

25. Snake Creek Cave, Snake Creek, South Snake Range, White Pine Co., Nevada. T12N, R70E. 17 August 1993, *Myotis ciliolabrum* (1 scrotal male, 3 females), *M. californicus* (1 lactating female), *M. evotis* (1 male, 1 female), *M. volans* (1 female), *Corynorhinus townsendii* (1 scrotal male), *Antrozous pallidus* (3 scrotal males).

26. Pescio Cave, Schell Creek Range, White Pine Co., Nevada. T19N, R64E. 18 August 1993, *Myotis ciliolabrum* (2 scrotal males), *M. californicus* (1 scrotal male, 2 females), *Eptesicus fuscus* (1 scrotal male), *Corynorhinus townsendii* (1 scrotal male, 1 lactating female).

27. Mine shafts near Emigrant Canyon, Edna Mountain, Humboldt Co., Nevada. T36N, R40E, sec 36. 1400 m. 28 Sept. 1993, *Myotis volans* (1), *M. ciliolabrum* (2), *Corynorhinus townsendii* (3).

28. North Fork Little Humboldt River, 3.5 mi S and 9 mi E of Table Mountain, Santa Rosa Range, Humboldt Co., Nevada. T44N, R41E, sec 1. 2270 m. 10 August 1991, *Lasionycterus noctivagans* (1).

29. Elko, town center, Elko Co., Nevada. T34N, R55E, center sec 15. 22 Sept. 1992 and 23 Sept. 1991, *Lasionycterus noctivagans* (1); 15 May 1992, *Pipistrellus hesperus* (1); 19 Aug. 1991, *Myotis ciliolabrum* (1); 15 July 1992, *Eptesicus fuscus* maternity roost; 15 Nov. 1994 and 6 Jan. 1995, *Tadarida brasiliensis* (2).

30. Mine shaft near Contact, Elko Co., Nevada. T45N, R64E, sec 19. 1800 m. 21 Dec. 1993, *Corynorhinus townsendii* (3 hibernating).

31. Cave in Spring Valley, White Pine Co., Nevada. T15N, R68E. 2300 m. 27 July 1994, *Tadarida brasiliensis* roost (54,000–82,000).

32. Murphy Wash, South Snake Range, White Pine Co., Nevada. T10N, R68E, sec 2. 2250 m. 29 July 1994, *Corynorhinus townsendii* (3), *Lasionycterus noctivagans* (1), *Myotis evotis* (11), *M. volans* (42), *Myotis* spp. (2), *Eptesicus fuscus* (1), *Tadarida brasiliensis* (1); 21 Sept. 1994, *Myotis volans* (35), *M. evotis* (4), *M. ciliolabrum* (1).

33. Rock Creek, Sheep Creek Range, Eureka Co., Nevada. T34N, R48E, sec 8. 1450 m. 21 May 1994, *Myotis ciliolabrum* (10), *M. evotis* (1).

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[3] Because of the sensitivity of natural caves, location descriptions are limited to township and range information.

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NUPTIAL, PRE-, AND POSTNUPTIAL ACTIVITY OF THE THATCHING ANT, *FORMICA OBSCURIPES* FOREL, IN COLORADO

John R. Conway[1]

ABSTRACT.—Observations and excavations of thatching ant nests from 1990 to 1994 at 2560 m in Colorado provided information on the numbers and behavior of males and winged and wingless queens. Nuptial activity was compared to that reported by other investigators at lower altitudes. Reproductives were observed from 24 June to 15 August. Activity was greatest in 1993 when reproductives were on 10 of 98 mounds in the area. Mating and swarming occurred on rabbitbrush 4 m from 1 nest 2–6 July. The number of wingless queens in 4 excavated nests varied from 0 to 198.

Key words: nuptial flight, Formica obscuripes, *Colorado, thatching ant.*

Information on the reproductive activity of the thatching ant, *Formica obscuripes* Forel, in Colorado is sparse (Gregg 1963). The purpose of this study is to help remedy the deficiency and to compare nuptial and pre- and postnuptial activity of the thatching ant at high altitude in Colorado with similar studies on this species at lower elevations in North Dakota (McCook 1884, Weber 1935, Kannowski 1963, Wheeler and Wheeler 1963), Michigan (Talbot 1959, 1972), Illinois (Herbers 1978, 1979), Idaho (Cole 1932), and Nevada (Clark and Comanor 1972). The Nevada site north of Reno at 1550 m most closely approximates the Colorado study area in elevation and vegetation.

Mating flight plays a major role in the reproduction and dispersal of most social insects (Holldobler and Wilson 1990). Males and queens of *F. obscuripes* fly to "swarming grounds" as reported by Talbot (1972). There males fly back and forth in search of queens, which alight on low vegetation and release pheromones to attract males (Cherix et al. 1993).

MATERIALS AND METHODS

The main Colorado study area (64.6 × 114 m) has 85 mounds and is dominated by big sagebrush (*Artemisia tridentata* Nuttall). It is adjacent to a quaking aspen grove (*Populus tremuloides* Michaux) at an elevation of about 2560 m. The site is located in Gunnison County north of Blue Mesa Reservoir and west of Soap Creek road. Other plants in the study area are *Chrysothamnus nauseosus* (Pallas) Britton (rubber rabbitbrush), *Purshia tridentata* (Pursh) de Candolle (antelope bitterbrush), *Lupinus argenteus* Pursh (silvery lupine), *Symphoricarpos rotundifolius* A. Gray (mountain snowberry), *Rosa woodsii* Lindley (Woods rose), *Urtica gracilis* Aiton (stinging nettle), *Penstemon strictus* Bentham (Mancos penstemon), *Ipomopsis aggregata* (Pursh) Grant ssp. *aggregata* (trumpet gilia), 1 Saskatoon serviceberry tree (*Amelanchier alnifolia* var. *pumila*), and 1 Douglas-fir (*Pseudotsuga* sp.). Observations in this area took place on 5–6 August 1990; 20–28 June, 22–27 July, 13–15 August, 12–13 September, and 11 October 1992; 28 June–16 August 1993; and 29 June–31 July and 14–16 August 1994. Observations before 20 June were not possible due to academic commitments. A nest was excavated on each of the following dates: 6 August 1990, 27–28 June 1992, 12–14 July 1993, and 11–25 July 1994. The 1993 mound was poisoned with 1 1/2 cups Hi-Yield ant killer granules (Diazinon) wetted down with about 2 gal of water prior to excavation.

RESULTS AND DISCUSSION

Reproductives

Reproductives (males, winged and wingless queens) were observed in Colorado from 24 June to 15 August over 3 summers. Activity was greatest in 1993 when reproductives were found on 10 mounds scattered among 98 nests in the area: males, winged queens, and wingless queens on 5 mounds; males and winged queens on 3 mounds; a winged queen on 1 mound; and a wingless queen on 1 mound. Observations of both male and female alates on Colorado mounds support Herbers's (1978) observations that some nests produce a mixture of sexes. We were unable to confirm reports that some nests produce all males or all females (Kannowski 1963, Herbers 1978), or that a changeover from early all-male flights to later all-female ones occurs (Talbot 1959, 1972, Clark and Comanor 1972).

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MALES.—Males were observed on 8 mounds from 28 June to 13 July 1993 and at 1 mound on 5–6 July 1994. Males seemed to prefer the shady side of 1 mound built around a fencepost. Workers sometimes chased males and once one carried a male on a mound. Others have reported males earlier in the year. Talbot (1959, 1972) saw males flying 16–24 June, and Clark and Comanor (1972) saw males from 15 April to 4 May.

Although males were observed from 0740 to 1635 hours in Colorado, they were most numerous and flew from 0938 to 1101. Talbot (1959) saw them fly even earlier, between 0608 and 1000. Clark and Comanor (1972) also saw morning flights, but noted males throughout the day (0840 to 1445).

The largest number of males on 1 Colorado mound was 10 on 3 July 1993, about the same maximum per mound (12) reported by Clark and Comanor (1972). Herbers (1979) noted up to 1264 males. Talbot (1959, 1972) reported even more males (up to 4500) but noted that the ratio of males to females varies from colony to colony and from flight to flight.

One male was found in a Colorado nest excavated in July 1993; none were in 3 other excavated nests. Wheeler and Wheeler (1963) reported males in nests from 23 May to 12 July.

WINGED QUEENS.—Winged queens were observed on 9 Colorado mounds from 28 June to 16 July 1993, and one was on a mound on 5 July and 10 July 1994. Workers pulled queens by their wings and antennae on mounds and were in turn sometimes dragged by queens. Queens were noted with tattered, spread, and partial wings from 30 June to 6 July. Others reported winged queens at nests earlier and later in the season than in Colorado. Clark and Comanor (1972) saw them as early as 1 May, and Wheeler and Wheeler (1963) reported winged females in nests as late as 8 August.

Winged queens were observed from 0654 to 1640 hours in Colorado, but most often in the morning. Clark and Comanor (1972) also saw them throughout the day, from 0830 to 1720. Those found later in the day were presumably remnants of the morning activity.

The maximum number of winged queens on 1 Colorado mound was about 50 on 3 July 1993. Others reported greater numbers per nest: 78 (Clark and Comanor 1972) and 230 (Talbot 1959). Winged queens were more abundant than males on Colorado mounds as reported by Clark and Comanor (1972), except on 1 occasion when males were more numerous. No winged queens were found in 4 excavated Colorado nests.

WINGLESS QUEENS.—Dealation was not observed in Colorado, but wingless queens were seen on 6 mounds and on trails from 24 June to 15 August between 0757 and 1742 hours. The greatest number on 1 mound was 7. Wingless queens were usually surrounded by a group of workers on the mounds who often pulled them by their antennae and legs and sometimes lunged at queens as if attacking them. Some were carried on the trails by workers. Dead wingless queens were observed being carried on a mound and a nearby dirt road.

The number of wingless queens in 4 nests excavated in Colorado varied greatly: 0, 1, 32, and 198. Five of the 198 queens from 1 nest were found with numerous workers amid a clump of rabbitbrush roots 1.5 m away from the excavated mound. Workers probably moved the queens along a trail from the main nest to a secondary nest at the rabbitbrush for safety during the prolonged excavation.

Kannowski (1963) stated that many species of *Formica* have more than 1 dealate queen per colony, and Cole (1932) reported 2 or more per *F. obscuripes* nest. The significance of the highly varible number of dealated queens per Colorado nest is unclear, and more excavations are necessary to determine the normal state of affairs. Observations of wingless queens on trails suggest that they may be transferred between mounds or adopted by existing colonies after the nuptial flight (Weber 1935).

Flight Season and Period

The time of year during which alates of a species in a given area fly is termed the flight season. Kannowski (1963) noted that species such as *F. obscuripes*, with a large geographical distribution, may have a very long flight season over their range. In Colorado, queens flew 1–8 July and males 1–9 July. Although others noted flights as early as 1 May (Clark and Comanor 1972) and as late as September (McCook 1884), flights were more common in June and July (Cole 1932, Weber 1935, Talbot 1972). Talbot (1972) noted that the flight season varies greatly from colony to colony in any year and that colonies may have 5–16 flights. Interestingly, she found that colonies in sheltered nests or those on west-facing slopes flew later than those on open east slopes.

Each ant species has a flight period—the time of day that flights take place. Kannowski (1959) reported that most species of *Formica* have early morning flights. Queens flew between 0950 and 1141, and males between 0938 and 1101 in Colorado. Colorado flights did not begin as early (0500) or end as early (0750) as some reported by Talbot (1959) in Michigan, perhaps due to colder temperatures at high altitude in the morning. Reproductive activity subsided at Colorado nests between 1040 and 1107, or approximately at the same times (1030–1145) reported by Talbot (1972).

Emergence and Positioning

Reproductive emergence and positioning behavior in Colorado is similar to that reported by Kannowski (1963) and Weber (1935). Alates emerged, walked around, and went back into the entrances before leaving the mound and climbing nearby structures. Workers sometimes chased emerging alates or held onto their wings; at other times they seemed to ignore the sexuals. Males ignore winged queens at this time. Winged queens left Colorado mounds 1–8 July 1993 between 0818 and 1145 hours. Winged queens and males were found on the ground as far away as 7.85 m and 5.28 m from the mounds, respectively.

Reproductives often climb prior to flight. In Colorado they climbed nearby sagebrush, rabbitbrush, lupine, and grass, as well as dead sagebrush and a fencepost protruding from mounds. At the most active mound they climbed 3 sagebrushes, 0.48–0.89 m high, and 0.91–2.57 m away. Others have reported alates on nearby sagebrush and rabbitbrush (Clark and Comanor 1972), grass and herbs (Weber 1935), and timothy and bluegrass (Talbot 1959).

Although a number of Colorado reproductives flew from their perches, many did not. Some queens descended 1–6 min after arrival, and one was pulled down by workers. Kannowski (1963) saw some alates wait longer (10–30 min) before flying from their perches. Tapping and blowing on perched queens did not induce them to fly.

A correlation between temperature and emergence and positioning was noted by Talbot (1972). She reported that alates began leaving mounds when the air temperature reached 17.2° C and began climbing plants at temperatures above 18.3° C.

Flights

In Colorado alates flew from grass, sagebrush, rabbitbrush, and lupine; a few took off from the ground. Prior to flying, some queens released their front legs and fanned their wings, as reported by Kannowski (1963). On the other hand, Talbot (1959) reported that queens flew quickly with little preliminary wing fluttering.

One Colorado queen flew east at least 13.1 m at an estimated altitude of 4 m. Another flight lasted about 20 sec at an estimated altitude of 9 m. Other winged queens moved away from mounds by alternately walking on the ground and making short, low flights between plants. One queen using this method moved 7.85 m away from a mound over a period of 37 min. Most queen flights were low and downhill to the east. Males generally had short (2.5 cm–1.5 m), flitting or hovering flights about a meter above the ground, sometimes relanding on the same vegetation from which they departed.

Reproductive activity was greatest in Colorado on clear, warm, windless days. All investigators agree that these are the most favorable conditions for flight. Wind supressed reproductive activity at 0918 hours on 3 July 1993. Weber (1935) noted alates leaving the nest when the air temperature was above 15.5° C, humidity exceeded 50%, and the sky was clear. Others reported first flights at an air temperature at least 5° C higher. A Colorado male flew at 22.7° C. Talbot (1972) reported that alates flew at temperatures between 20.5° C and 27.2° C, and Clark and Comanor (1972) saw flights between 20.5° C and 26.5° C, but at a relative humidity of only about 18%. Talbot (1959, 1972) noted that wind gusts, rain, low temperatures, and dark skies stopped flights, and wet grass and gray skies delayed flying.

Colorado flights involved relatively few reproductives, but reports in the literature vary considerably. Weber (1935) believed there is no marriage flight because only 1 sexual or a few sexuals fly at a time. Kannowski (1963) saw 1 mass flight, but noted most flights were sparse or moderate. Talbot (1959), on the other hand, reported that 695 females and an estimated 4500 males flew over time. Rates of flying of 4–14 queens/min and 1–10 males/min have been reported (Talbot 1959, Clark and Comanor 1972).

There appears to be no agreement on the flight pattern. Talbot (1959) noted that most queens flew downhill and westward, but some had short, sporadic flights from plant to plant or to the ground as sometimes observed in Colorado. Colorado flights were generally at low altitude (estimate 4–9 m), downhill, and eastward toward the sun. Kannowski (1963) also noted that alates fly in the general direction of greatest light intensity. Others report that flights are often upward and out of view (12 m or more; Weber 1935, Kannowski 1963, Clark and Comanor 1972).

Swarming and Mating

Swarming is the process whereby alates aggregate to mate in the air or on the ground and vegetation (Kannowski 1963). Most swarming and mating in Colorado occurred 2–6 July 1993 between 1008 and 1125 hours on rabbitbrush 4.01 m from 1 mound. Mating was also observed on rabbitbrush beside another mound on 2 July and 6 July 1993. Talbot (1972) noted swarming earlier in the year and over a longer time period, namely, 4–17 June between 0700 and 1200.

Swarming in Colorado was similar to that described by Kannowski and Johnson (1969) and Talbot (1972). Queens arrived first on rabbitbrush, followed by males. Queens perched on the upper parts of plants often with their heads down and their abdomens pointing upward or toward the nest. Presumably they emit a pheromone to attract males (Kannowski and Johnson 1969, Walter et al. 1993). Once the female's pheromone is detected, males fly upwind to the general location of the female, fly quickly from stem to stem until they find her, alight, and then attempt to mate (Kannowski 1963). After mating, males usually fly off while the queen remains and sometimes inspects her abdomen.

Up to 7 in copulo alates were noted at 1 time at the Colorado swarming site 4.01 m away, 6 pairs on rabbitbrush and 1 pair on an adjacent lupine. Some pairs fell off the plants. One queen appeared to mate 2 or 3 times. Kannowski (1963) reported a queen mating 4 times. Two Colorado males tried to simultaneously mate with a queen for 1 min 40 sec and remained attached to each other for 20 sec after the queen left. Talbot (1972) noted 3 or 4 males trying to mate a queen, and Kannowski (1963) reported a single male may mate several times before flying away.

The durations of 6 Colorado matings ranged from 1 min 40 sec to 3 min 40 sec (mean = 2 min 43 sec), or within the 1- to 5-min durations reported by Talbot (1972).

Talbot (1959, 1972) noted larger, more diverse, and more heavily populated swarming areas than the small rabbitbrush area in Colorado. Some of her swarming areas were over short grass; others were on shrubs. One swarming area involved thousands of males hovering over hundreds of females from 3 colonies and covered an oval-shaped area 27.5 × 11 m. Males usually flew near grass level, but sometimes as high as 1.2–1.5 m. Another swarming area shifted somewhat from day to day and increased to approximately 41.3 × 32.1 m. She found that these areas were maintained throughout the flying season, and some were used year after year.

CONCLUSIONS

Preliminary studies of the reproductive behavior of the thatching ant, *F. obscuripes*, in Colorado are in general agreement with the literature. Time constraints on our seasonal observations probably explain why we did not observe reproductive behavior as early in the year as that reported in the literature. The most notable finding was the paucity of reproductive activity: swarming and mating were observed only 2–6 July 1993; 9 of 98 mounds (9%) in the area had winged reproductives; mating occurred near 2 mounds (2%); and a swarming area was found 4.01 m from 1 mound (1%). The numbers of males and winged queens were relatively low and the swarming area was small. Other notable findings were the highly variable number (0–198) of dealated queens per nest and the almost complete absence of winged alates in excavated nests.

Further studies are needed to determine whether our findings are anomalies or whether they represent the normal state of affairs for this species at high altitude.

ACKNOWLEDGMENTS

I thank 4 University of Scranton students, John Bridge, Tom Sabalaske, Anthony Musingo, and Jeanne Rohan, who conducted fieldwork in Colorado in 1993–94. Support for this research was provided by a grant from the Howard Hughes Medical Institute through the Undergraduate Biological Sciences Education Program. Barry C. Johnston, ecologist at the U.S. Forest Service in Gunnison, Colorado, identified plant specimens.

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TRACHYTES KALISZEWSKII, N. SP. (ACARI: UROPODINA), FROM THE GREAT BASIN (UTAH, USA), WITH REMARKS ON THE HABITATS AND DISTRIBUTION OF THE MEMBERS OF THE GENUS *TRACHYTES*

Jerzy Błoszyk[1] and Paweł Szymkowiak[1]

ABSTRACT.—*Trachytes kaliszewskii*, n. sp., is described from the Great Basin, Utah, USA. SEM photography illustrates morphological detail. An annotated list is included of currently recognized species of the genus *Trachytes*, with comments on their distribution and habitat characteristics.

Key words: mites, Trachytes kaliszewskii, *Uropodina, Great Basin, Utah.*

Mites of the genus *Trachytes* Michael, 1894, are a morphologically distinct entity of the Uropodina. The genus consists of 31 species known mainly from the Palearctic region of Europe and Japan. Wiśniewski and Hirschmann (1993) mention two species from the USA: *T. aegrota* (C. L. Koch, 1841) and *T. traegardhi* (Hirschmann and Zirngiebl-Nicol, 1969). *Trachytes traegardhi* is regarded as *nominum nudum*. The USA listing for *T. aegrota* is considered either a mistake in determination or an accidental introduction.

Taxonomic studies on mites of the genus *Trachytes* are found in Hirshmann and Zirngiebl-Nicol (1969), Huţu (1983), and Pečina (1970). Information on their biology, ecology, and zoogeography is found in Athias-Binche (1978, 1979, 1980, 1981, 1985), Pečina (1980), Błoszyk (1980, 1982, 1984, 1985, 1990, 1991, 1992, 1993), Błoszyk and Athias-Binche (1985), Błoszyk and Miko (1990), Błoszyk and Olszanowski (1985a, 1985b, 1985c, 1986), and Błoszyk et al. (1984).

We found a new species of the genus *Trachytes* in soil collected from Rock Canyon near Provo, Utah, USA. It is most similar to those described by Hiramatsu (1979, 1980) from Japan: *T. aoki* and *T. onishii*. Morphological differences between our species, those mentioned from Japan, and *Trachytes aegrota* are shown in Table 1. Our new species is dedicated to the Polish acarologist, Dr. Marek Kaliszewski, who was a faculty member at Brigham Young University, Provo, Utah, USA, until 1993, when he died tragically in an automobile accident.

SYSTEMATIC STATUS OF THE GENUS *TRACHYTES* MICHAEL

SUPERFAMILY.—Polyaspidoidea sensu Athias-Binche & Evans, 1981

FAMILY.—Trachytidae Trägårdh, 1938

GENUS.—*Trachytes* Michael, 1894

TYPE SPECIES.—*Celano aegrota* C. L. Koch, 1841 (=*Trachynotus pyriformis* Kramer, 1876)

Mites of middle size, strongly sclerotized, dorsoventrally flattened. Idiosoma triangular, "vertex" distinct with smooth or slightly serrated edges. Corniculus simple, laciniae longer than corniculi. Hypostomatic setae: ***h1*** very long, simple; ***h2*** shorter than ***h1***, simple; ***h3*** very long, massive; ***h4*** very short, serrated. Fixed digit of the chelicera longer than moveable digit, sharply pointed distally. Base of tritosternum wide, not covered by coxae I.

Trachytes kaliszewskii, n. sp.

DIAGNOSIS.—The form of the body is typical for the genus *Trachytes* Michael. Vertex with lamella. Dorsal shield with polygonal pattern and irregular cavities in central part (similar to *T. aegrota*). Marginal shield is not divided as in European species, without polygonal pattern. Dorsal setae long and massive. Small pygidial shield present in female. Epigynial shield trapezoidal with net pattern, front margin slightly convex and produced laterally into little corns. Sternal setae short. Operculum of male rounded, with a pair of long genital setae. Ventroanal shield separated from sternal and metapodal shields by a wide zone of interscutal membrane.

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Ventral setae long. One pair of paranal setae. Postanal seta present.

ADULT FEMALE.—Length of idiosoma 900–907 μm, width 535–574 μm.

Dorsum: Lamellae with characteristic pattern. Marginal shield not divided posteriorly, with irregular cavities in posterior part. Dorsal shield with polygonal pattern laterally and irregular cavities in central and posterior parts (Figs. 1, 10, 11). Dorsal setae long and massive. Two pairs of setae on vertex; no unpaired medial dorsal setae. Marginal setae on small scutellae; 4 pairs of setae situated medially on marginal shields. Pygidial shield with pattern as on marginal shield.

Ventrum: Sternal shield (Fig. 2) fused to parapodals. Ventroanal shield separated from sternal and metapodal shields by a zone of interscutal membrane bearing 4 pairs of platelets (Fig. 13).

Sternal shield smooth, bearing 5 pairs of short sternal setae. Setae: ***st*1** situated between coxae II at the level of their front margins; ***st*2** and ***st*3** placed above anterior edge of epigynium; ***st*4** and ***st*5** situated laterally of epigynium. Opisthogastric setae generally long, simple or delicately serrated, most anterior pair short, similar to sternal setae. First pair of opisthogastric setae situated below posterior margin of epigynium, 2nd pair on metapodal shields, with 4 pairs on interscutal membrane and 2 pairs on ventroanal shield. One pair of adanal setae; short and serrated. Postanal seta long. Exopodal and metapodal shields with oval or irregular cavities. Ventroanal shield smooth anteriorly, with polygonal patterns in the posterior regions.

Epigynial shield trapezoidal, with front margin slightly convex and produced laterally into little corns; measurements: 175–199 μm length and 137–156 μm width (N = 3). Surface of epigynium with delicate polygonal net in anterior and central areas.

Peritrema simple, without poststigmatic section, extending from the level of the posterior border of the foramen pedale III (with stigma) to beyond coxae II.

Gnathosoma: Laciniae (internal mala) longer than corniculi, serrated. Hypostomatic setae (Fig. 4) smooth except for setae ***h*4** which are delicately serrated; ***h*1** very long, ***h*2** shorter than ***h*1**, ***h*3** long as ***h*1** but more massive, ***h*4** shorter than ***h*2**. Three transversal rows of hypognathal denticles between setae ***h*3** and ***h*4**.

Appendages: Shape of chelicerae typical for *Trachytes;* fixed digit of the chelicera longer than moveable digit, shaped distally. Pedipalp ventral, setae of trochanter (**v1**, **v2**) massive and serrated (Fig. 5).

Shape of legs typical for family. Tarsi of legs II–IV with 4 long setae (3 times longer than

TABLE 1. Summary of major differences between closely related *Trachytes* species.

Character	*T. aegrota*	*T. aoki*	*T. onishii*	*T. kaliszewskii*
Sex	parthenogenic	bisexual	?	bisexual
FEMALE				
Lamella	transverse	transverse	transverse	oblong
Setae on interscutal membrane	absent	present	absent	present
Unpaired mediodorsal seta	present	absent	absent	absent
Body measurements (in μm)	600 × 685	400 × 450	400 × 600	535–574 × 900–907
Hypostomal setae h3	simple	massive	massive	massive
Setae on ventroanal shield	different	equal	equal	equal
Epigynium	smooth	smooth	with polygonal net	
Ventral seta on metapodal shields	long	short	short	long
Seta *Pa*	short	short	short	long

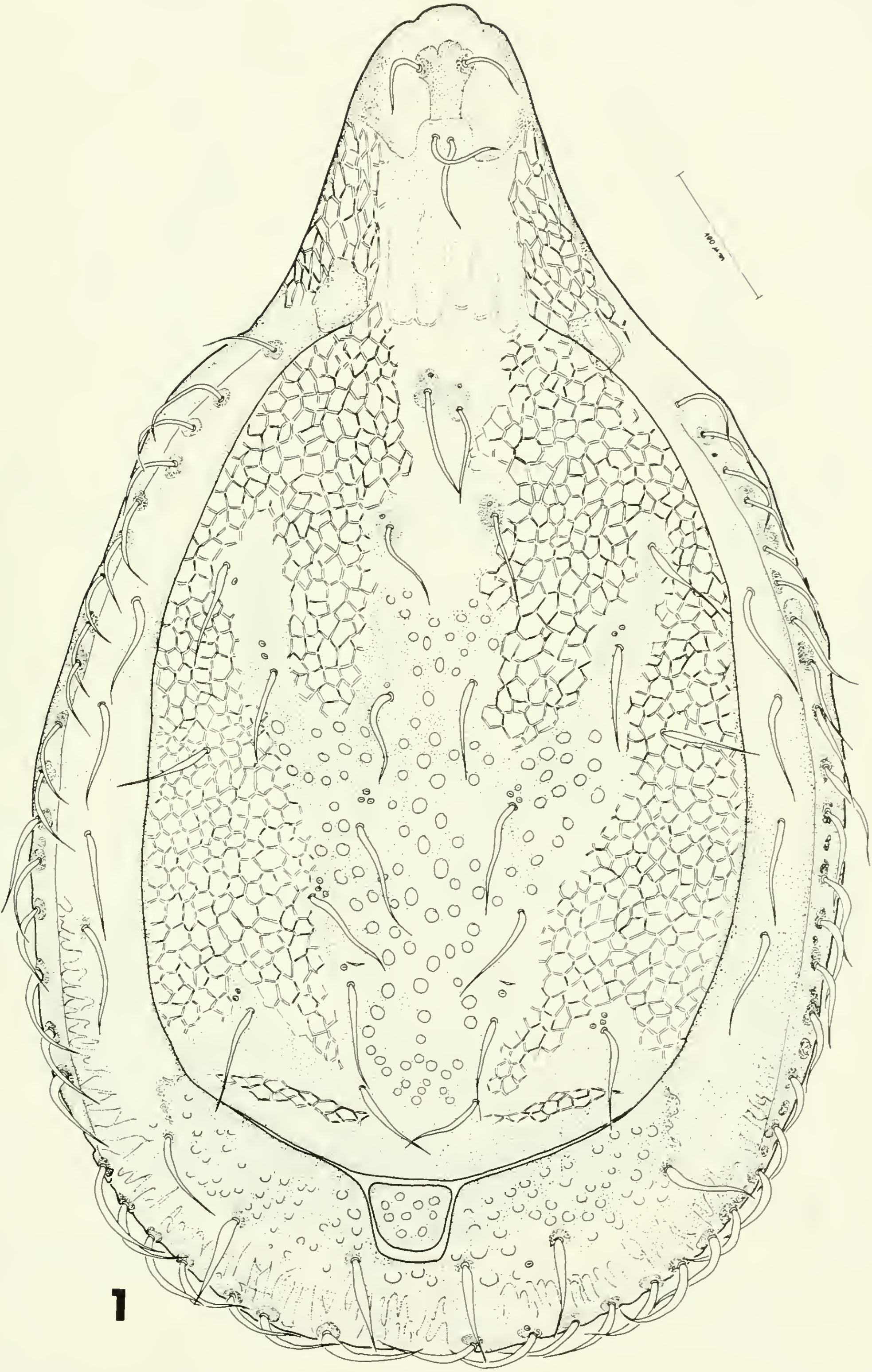

Fig. 1. *Trachytes kaliszewskii*, n. sp., dorsal view of female idiosoma.

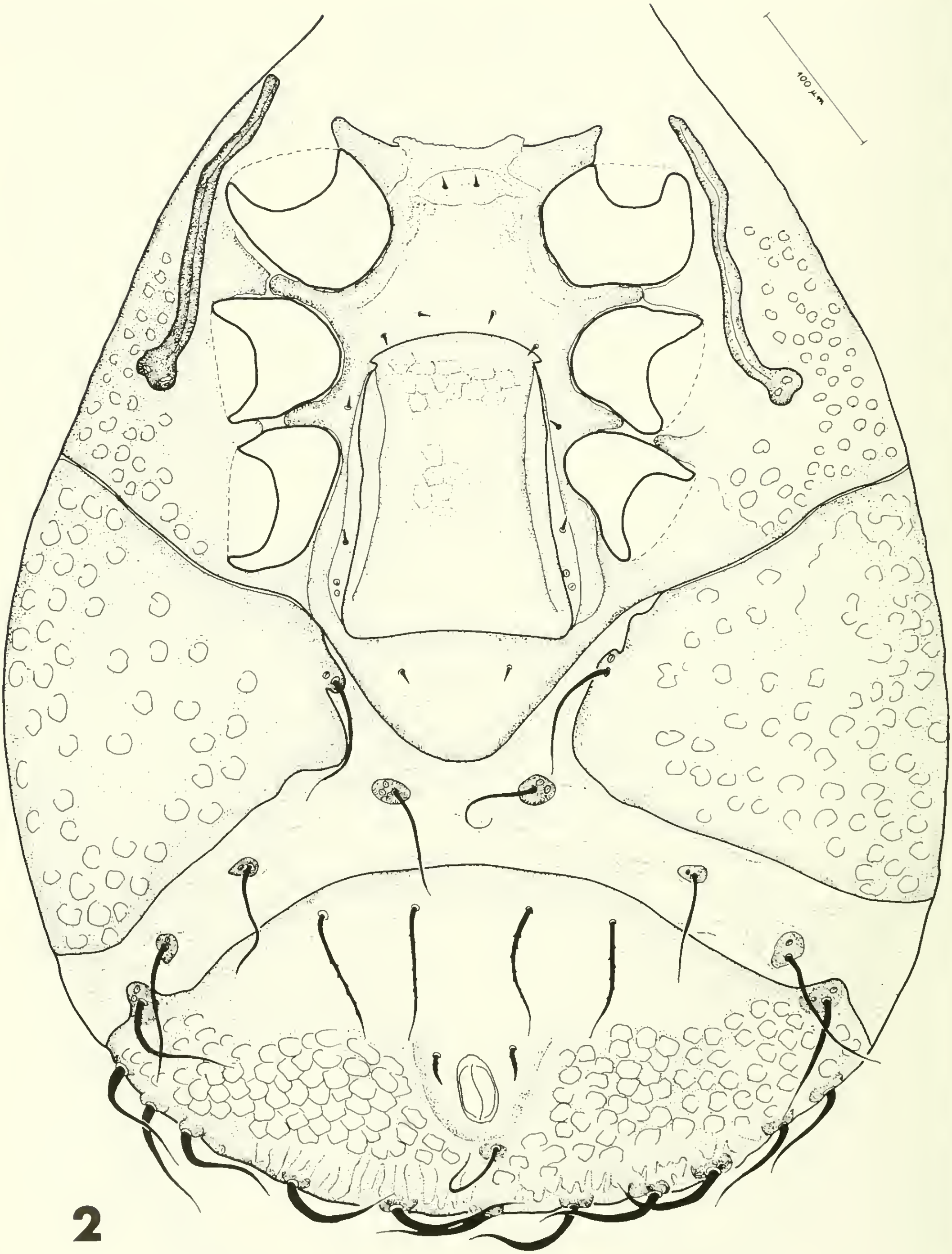

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Fig. 2. *Trachytes kaliszewskii*, n. sp., ventral view of female idiosoma.

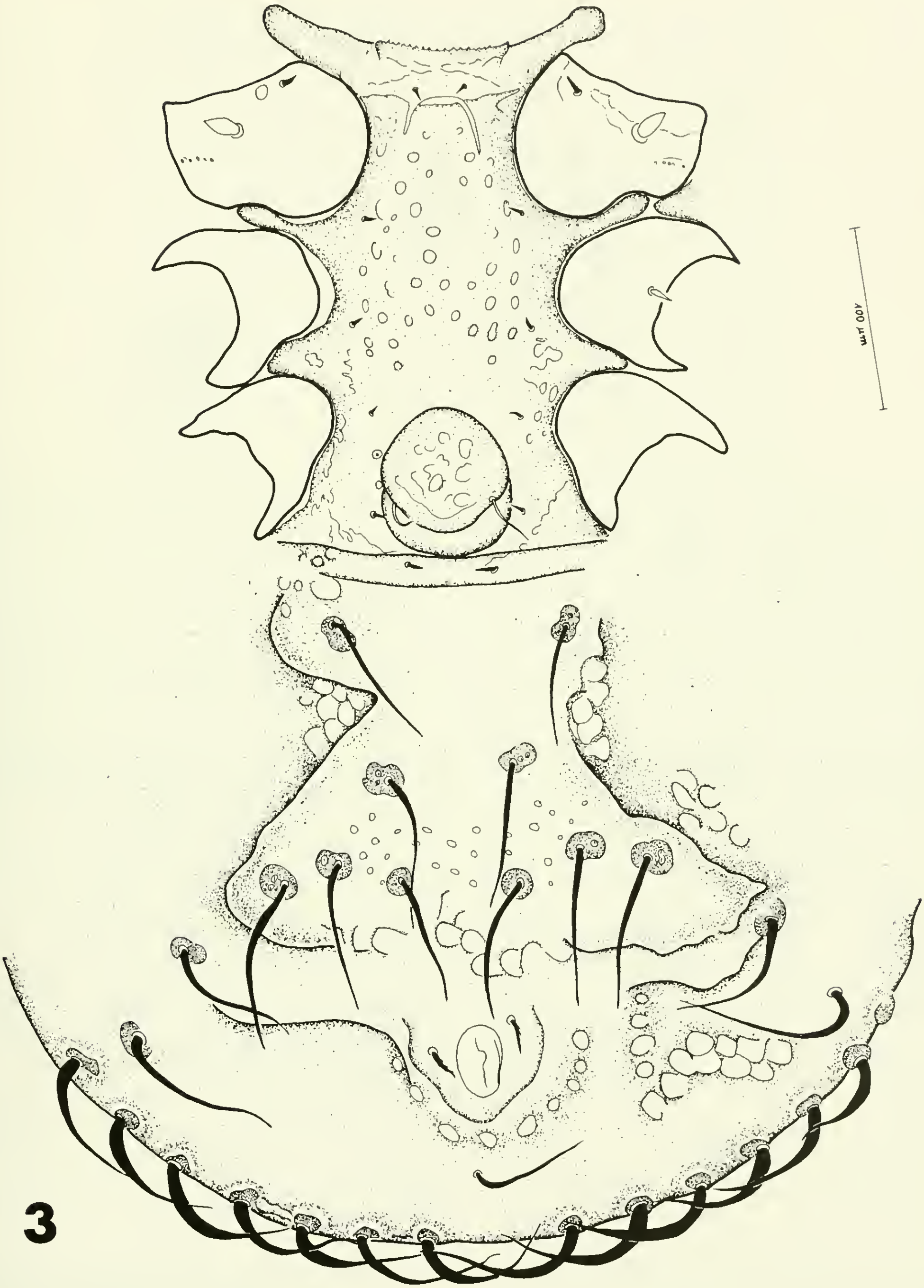

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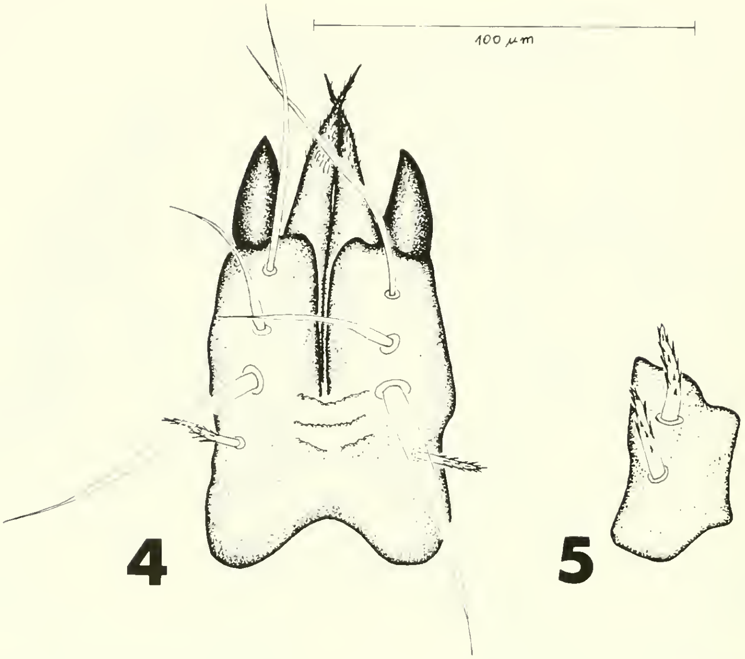
Fig. 3. *Trachytes kaliszewskii*, n. sp., ventral view of male idiosoma.



Figs. 4–5. *Trachytes kaliszewskii*, n. sp., female: 4, gnathosoma, ventral view; 5, ventral setae of palpal trochanter.

others), small claws, and a very long distal seta. Shape of dorsal setae on tarsus, tibia, genu, and femur of legs I as in the genera *Polyaspis* and *Polyaspinus*. Chaetotaxy of legs I and IV is shown in detail in Figures 6 and 7.

Sexual dimorphism observed on femora II (Figs. 8, 9).

ADULT MALE.—Body measurements 830–862 µm × 538–540 µm.

Dorsum: Male dorsum slightly changed in posterior part; pygidial shield absent (Fig. 12). Sculpture and dorsal chaetotaxy as in the female.

Ventrum: Sternal shield with numerous oval cavities and bearing 5 pairs of short sternal setae (Fig. 3). Genital operculum rounded (74–79 × 72 µm), located a little below coxae IV, with 1 pair of long genital setae. Opisthosoma separated by transverse suture with interscutal membrane. Seven pairs of long ventral setae on rounded platelets; 1st pair short, located below operculum. With 1 pair of delicately serrated adanal setae and long unpaired postanal seta (**Pa**). Opisthosoma with polygonal sculpture on metapodal and anal shields and small oval cavities on central portion.

DEUTONYMPH.—Body measurements 624 × 396 µm.

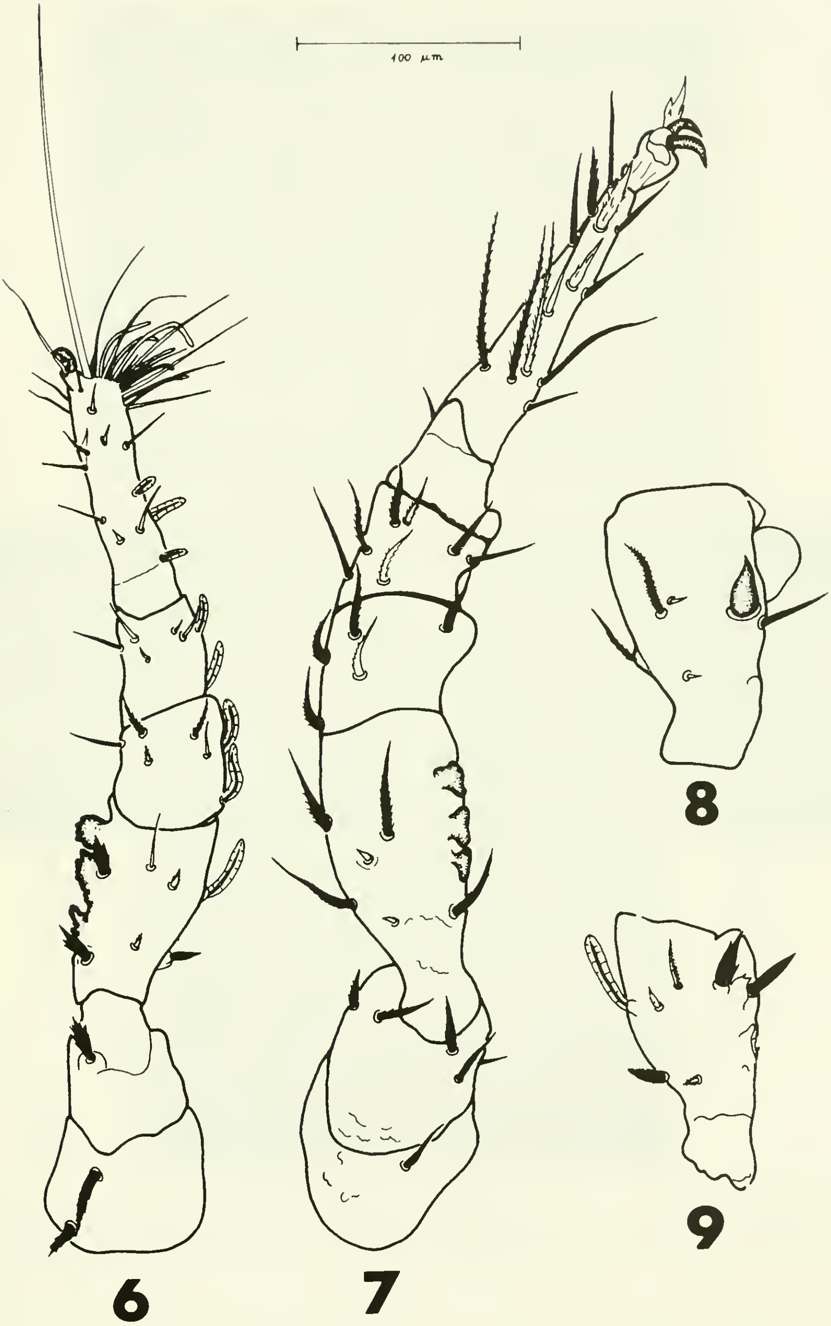
Dorsum: Dorsum with polygonal pattern (Fig. 15). Podonotal shield trapezoidal, fused with lamellae. Mesonotal shields large, triangular, with 4 setae. Pygidial shield arched, with 2 pairs of setae. Dorsal setae strong, massive. Setae on interscutal membrane and marginal setae inserted on small platelets.

Ventrum: Ventrum with polygonal pattern (Fig. 16). Sternal shield elongated, with 5 pairs of short sternal setae; most posterior pair delicately serrated. Opisthogastric setae situated on interscutal membrane, delicately serrated, sitting on small platelets. Large ventroanal shield with 2 pairs of short adanal setae (**Ad**), postanal seta (**Pa**) longer than **Ad**; both setae serrated.

PROTONYMPH.—Body measurement 528 × 295 µm.

Dorsum: Dorsum with polygonal pattern (Fig. 17). Podonotal shield trapezoidal. Mesonotal shields large, oval-triangular, without setae. Pygidial shield arched, with 2 strong, massive setae. Dorsal setae strong, massive. No setae on intersutal membrane. Marginal setae numerous, inserted on small platelets.

Ventrum: Sternal shield smooth, elongate, with 4 pairs of simple sternal setae (Fig. 18). Four massive, serrated opisthogastric setae

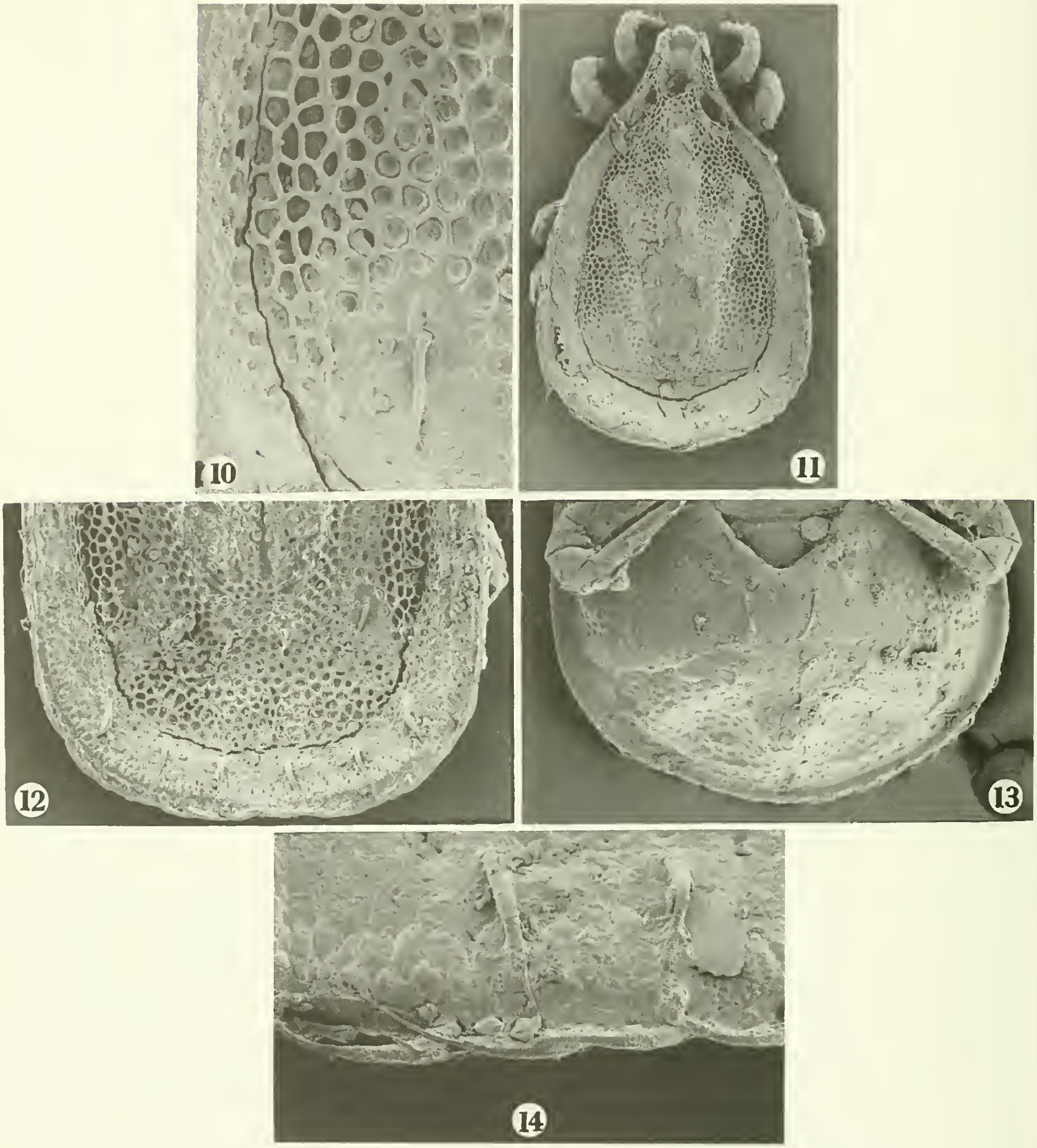


Figs. 6–9. *Trachytes kaliszewskii*, n. sp., legs chaetotaxy: 6, leg I of female; 7, leg IV of female; 8, chaetotaxy of male femora II; 9, chaetotaxy of female femora II.

situated on intersutal membrane. Large ventroanal shield with 1 pair simple adanal setae and a long postanal seta.

MATERIAL EXAMINED.—All specimens were collected from soil under a maple tree in Rock Canyon near Provo, Utah, 10 September 1992; leg. J. Błoszyk (holotype and 5 paratype females, 7 paratype males, 7 deutonymphs, 5 protonymphs).

The holotype is deposited in the Canadian National Collection, Biosystematics Research Centre, Ottawa, Canada. Paratypes are deposited



Figs. 10–14. *Trachytes kaliszewskii*, n. sp.: 10, dorsal polygonal pattern of female (550X); 11, female, general dorsal view (110X); 12, posterior part of male idiosoma (220X); 13, opisthosoma of female (200X); 14, marginal setae of female (750X).

in the Monte L. Bean Life Science Museum, Brigham Young University, Provo, Utah, USA; in CSIRO, Canberra, Australia; and in J. Błoszyk's collection (Acarological Association, ul. Lisowskiego, 16/1, 61-606 Poznań, Poland).

LIST OF THE *TRACHYTES* SPECIES WITH REMARKS ON DISTRIBUTION AND HABITAT PREFERENCES

Hirshmann (1993) listed 31 species referable to the genus *Trachytes*. In view of the

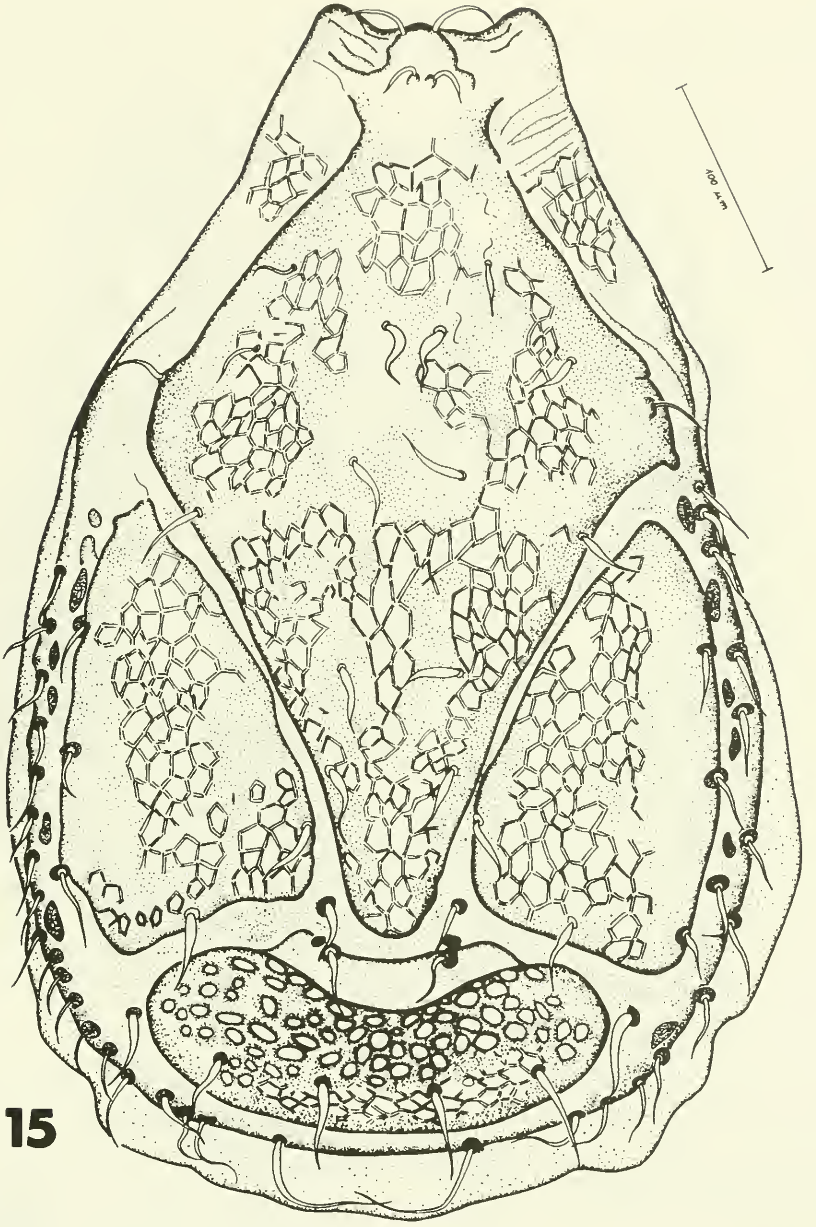


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Fig. 15. *Trachytes kaliszewskii*, n. sp., dorsal view of deutonymph idiosoma.

above, we recognize 31 species in the genus *Trachytes* as follows[2]:

Trachytes aegrota (C. L. Koch, 1841) is one of the most numerous Uropodine species in central Europe. This species is parthenogenetic and nonphoretic; males are rarely found (sex ratio is 1:10,000). This eurytopic species lives in all kinds of biotypes, but it prefers forest litter. It most often occurs below 500 m elevation but is considered a tychoalpine species (i.e., lives in the mountains as well as the lowlands). In Poland the spring–summer season is the best time to observe the larva.

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[2] Some data from Poland originate from an unpublished investigation carried out by J. Błoszyk in the thematic program *Bank of Invertebrate Fauna*; data on the distribution may be found in Hirschmann (1979, 1993), Huţu (1973, 1983), Hiramatsu (1979, 1980), and Athias-Binche (1981).

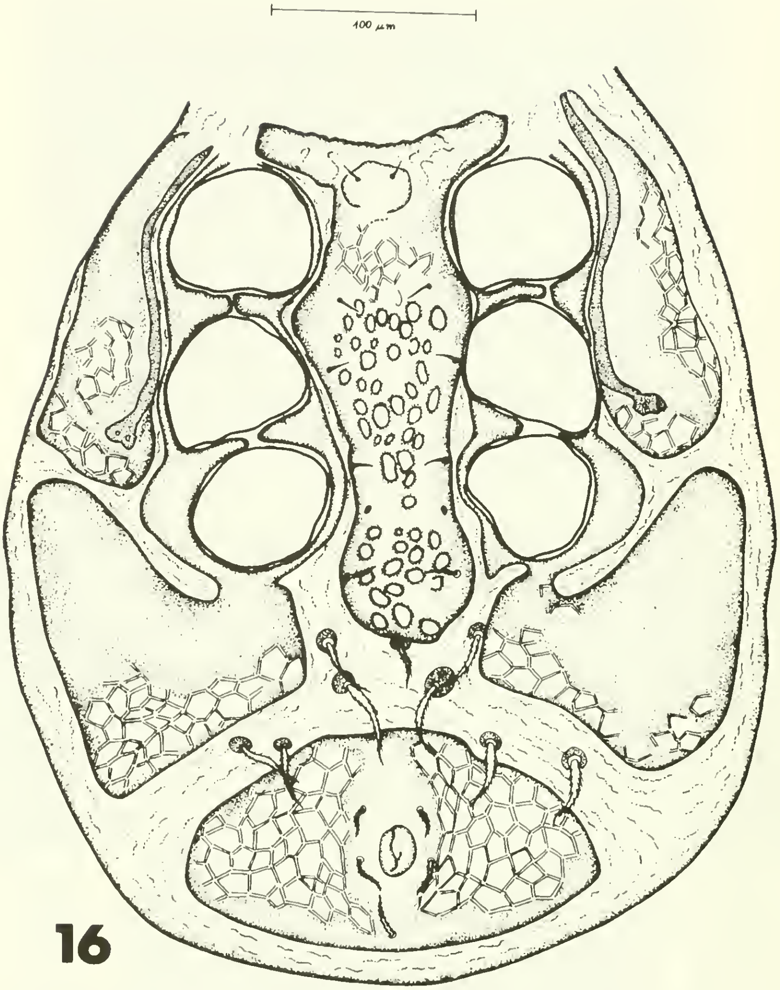

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Fig. 16. *Trachytes kaliszewskii*, n. sp., ventral view of deutonymph idiosoma.

Trachytes aoki Hiramatsu, 1979. Japan. In litter.

Trachytes arcuatus Hirschmann and Zirngiebl-Nicol, 1969. Austria, Romania, Hungary. Habitat unknown.

Trachytes baloghi Hirschmann and Zirngiebl-Nicol, 1969. Romania, Hungary. Habitat unknown.

Trachytes decui Huţu, 1983. Romania. In litter.

Trachytes edleri Huţu, 1983. Sweden. In grass.

Trachytes elegans Hirshmann and Zirngiebl-Nicol, 1969. Spain, Austria. Edaphic species.

Trachytes eustructura Hirshmann and Zirngiebl-Nicol, 1969. Spain and Austria. Associated with *Fabaceae*.

Trachytes hiramatsui Huţu, 1983. Romania. Habitat unknown.

Trachytes hirschmanni Huţu, 1973. Romania. In moss.

Trachytes hokkaidoensis Hiramatsu, 1983. Japan. Soil.

Trachytes inermis (Trägårdh, 1910). Sweden. In litter, moss, lichens, and under bark.

Trachytes irenae Pečina, 1970. A submontane species, reported from Czech Republic, Slovakia, Romania, Austria, Poland, and Yugoslavia. This species shows a considerable preference for beech and beech-fir forest litter. Poland is the northern limit of its distribution.

Trachytes lamda Berlese, 1904. Rare European species. Parthenogenetic and nonphoretic species—males found very rarely (sex ratio

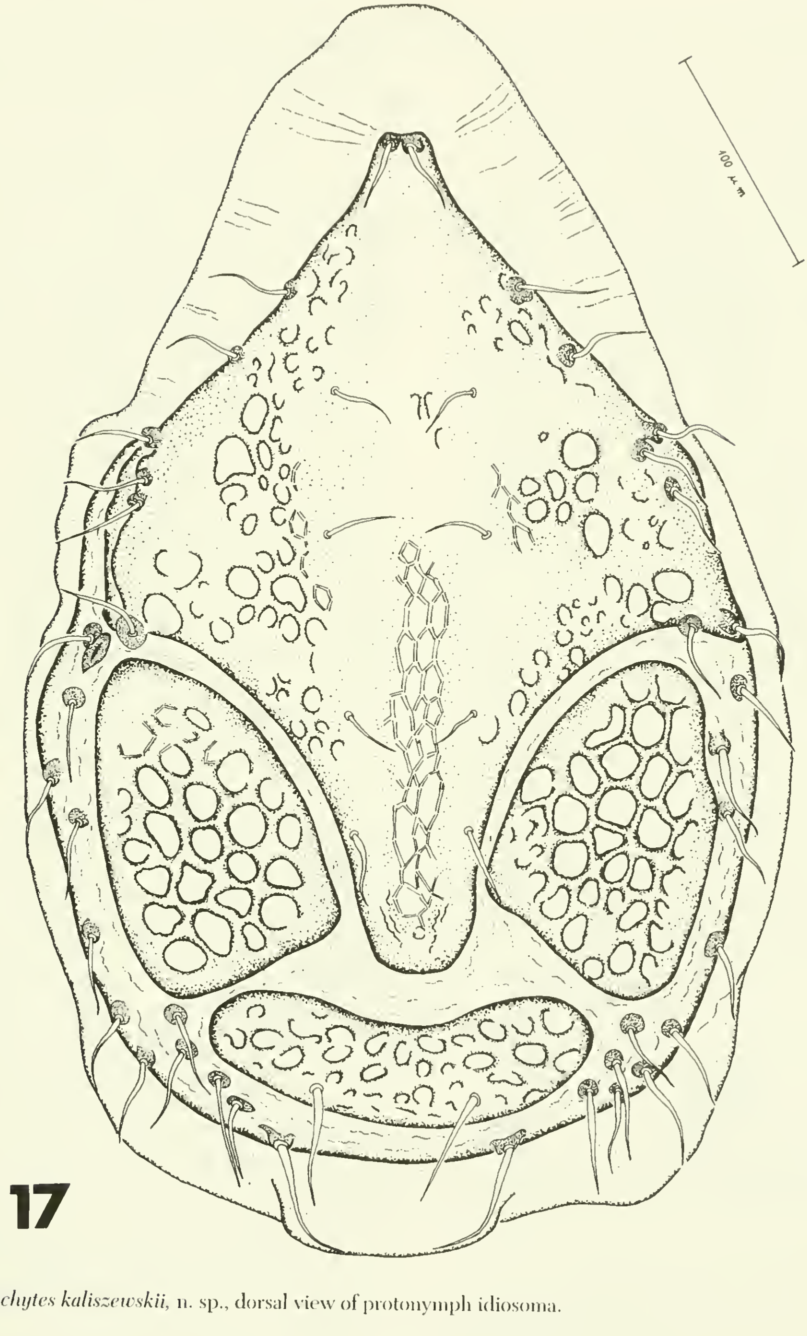

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Fig. 17. *Trachytes kaliszewskii*, n. sp., dorsal view of protonymph idiosoma.

1:400). Forest litter species typical of the beech forest and *Quercus-Carpinetum* forest. Not usually found above 500 m elevation.

Trachytes micropunctata Huţu, 1973. Romania. In litter

Trachytes minima Trägårdh, 1910 sensu Pečina 1970. Czech Republic, Slovakia, Poland, and Ukraine. Reports of this species in Sweden and Great Britain most likely refer to *Trachytes pauperior.* Poland is the northern limit of its distribution. *T. minima* prefers multispecies litter: deciduous forests, beech and beech-fir forests, brush, rock, and on grasses of calcareous ground. It is most commonly found

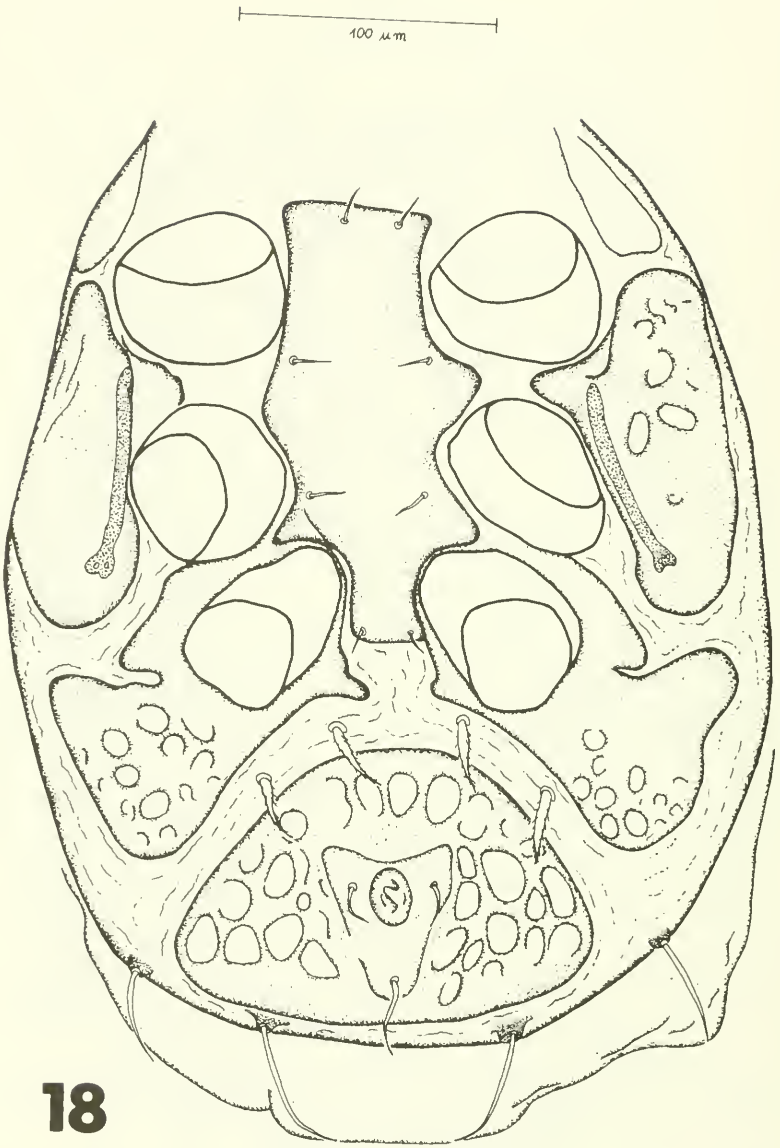

Fig. 18. *Trachytes kaliszewskii*, n. sp., ventral view of protonymph idiosoma.

between 300 and 900 m elevation. It is not found in the Tatra or Babia Góra Mountains.

Trachytes montana Willmann, 1953. High mountains in Austria, Czech Republic, Poland. This is a typical mountain species that prefers cold rocks and grasses on noncalcareous ground, spruce forest, dwarf-pine, beech, and fir-beech forest. Its optimum occurrence is at elevations above 1000 m.

Trachytes mystacinus Berlese, 1910. Italy, Switzerland, and Austria. Habitat unknown.

Trachytes onishii Hiramatsu, 1980. Japan. In litter.

Trachytes oudemansi Hirschmann and Zirngiebl-Nicol, 1969. Germany, Romania. In litter.

Trachytes pauperior (Berlese, 1914). Widely distributed European species but not as abundant as *T. aegrota*. *T. pauperior* is a parthenogenetic and nonphoretic species; males are rare as in the case of *T. aegrota* (sex ratio is 1:400). It appears in varied biotypes but most often in beech forest, multispecies deciduous forests, on grass, and on decalcified rocks. A tychoalpine species. The best time to observe the larva is during the spring–summer season.

Trachytes pecinaia Huţu, 1983. Romania. In litter.

Trachytes pi Berlese, 1910. West and Central Europe. In litter.

Trachytes romanica Huţu, 1983. Romania. In litter.

Trachytes splendida Huţu, 1983. East Carpathian species—Romania, Poland, Slovakia. In litter and moss.

Trachytes stammeri Hirschmann and Zirngiebl-Nicol, 1969. Locality and biotype unknown.

Trachytes tesquorum Pečina, 1980. Czech Republic. In grass.

Trachytes traeghardi Hirschmann and Zirngiebl-Nicol, 1969. Locality and biotype unknown.

Trachytes tubifer Berlese, 1914. Italy, Austria. In litter.

Trachytes welbournia Moraza, 1989. Spain. In litter.

Trachytes wisniewski Huţu, 1983. Romania. In litter.

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PRODUCTIVITY, FOOD HABITS, AND ASSOCIATED VARIABLES OF BARN OWLS UTILIZING NEST BOXES IN NORTH CENTRAL UTAH

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ABSTRACT.—Productivity and food habits of the Barn Owl (*Tyto alba*) utilizing nest boxes in Juab, Utah, and Salt Lake counties, Utah, during 1979–1984 were examined. Average clutch size was 5.8 eggs for the 6-yr period; mean number fledged was 3.9 young per successful nest. While severe weather during the 1981–82 winter did not result in a significant decrease in productivity during the 1982 breeding season, it may have resulted in a significant overproduction of female young. Barn Owls in north central Utah fed almost exclusively on mammalian species, particularly *Microtus* spp. Differences in clutch size between areas and years may be a response to availability as well as abundance of prey.

Key words: Barn Owl food, Barn Owl reproduction, nest boxes, Utah, Tyto alba.

The Barn Owl (*Tyto alba*) is a nearly cosmopolitan species that uses diverse nest sites, including man-made ones (Voous 1988). Although Barn Owls were reported in Utah as early as 1899 (Smith and Marti 1976), they were considered uncommon and rare breeders prior to 1976 (Smith and Marti 1976). The first Barn Owl nesting record was reported by Behle (1941) near Kanab in Kane County. Woodbury et al. (1949) proposed that Barn Owls were probably residents and widely distributed in valleys and lower elevations throughout the state. Smith et al. (1972, 1974) and Smith and Marti (1976) presented information on Barn Owl food habits, nesting ecology, and distribution throughout the state. While these studies indicated prey was abundant in irrigated agricultural areas, nesting sites were not adequate in those areas to allow growth of the population (Marti et al. 1979).

Marti et al. (1979) installed 8 nest boxes in abandoned concrete silos in north central Utah during 1977 and an additional 22 in 1978 in an effort to increase numbers of nesting Barn Owls. Of those boxes, 50% were used by breeding owls in 1977 and 80% in 1978. A total of 154 young fledged from nest boxes during the 2 yr.

In 1979 a similar program of installing nest boxes in silos was adopted in central Utah by the Utah Division of Wildlife Resources (UDWR). Between 1979 and 1984, 41 nest boxes were installed in Juab, Utah, and Salt Lake counties. An ongoing investigation of Barn Owl population and feeding habits was undertaken in 1979. Herein we document reproductive activities, dispersal, survival, and food habits of Barn Owls utilizing these nest boxes from 1979 to 1984.

STUDY AREA

This study was conducted on the 15- to 25-km-wide strip of farmland and suburban area between the Wasatch Mountains on the east and Utah Lake on the west. The climate is arid, characterized by hot, dry summers, cold winters, and cool, wet springs. Precipitation averages 40 cm annually, falling mainly as winter snow. Extensive agricultural irrigation and the presence of a large freshwater lake have created broad areas of habitat, especially for voles (*Microtus* spp.), a major Barn Owl prey. Trees occur sporadically along rivers and irrigation canals and on farmsteads.

Preliminary surveys by UDWR in 1979 revealed that 50 silos were used for roosts by Barn Owls, as indicated by presence of regurgitated pellets, fecal stain, and/or presence of owls. Silos were in rural or semirural areas throughout the counties and generally close to corn or alfalfa fields; a few were located in suburban areas within 2 km of an agricultural area (dairy or cattle ranch). Silos not used by farmers provided roosting owls protection from predation and disturbance; however, none provided adequate nest sites. Most barns and other structures in the area also lacked adequate nesting sites.

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Forty-one wooden nest boxes were built, after Marti et al. (1979), and installed between 1979 and 1984 (18 installed in 1979, 6 in 1980, 5 in 1981, 9 in 1982, and 1 each in 1983 and 1984). Three nest cavities (2 in silos and 1 in a school building) were discovered and monitored during these years; data from these sites are included herein.

METHODS

All nest boxes were examined at least once monthly throughout the year to determine presence of adult owls or fresh regurgitated pellets. Behavior of adults was recorded on all visits, and adults were caught and banded if possible. Pellets were collected during each visit. Presence of cached food and prey remains inside boxes and on silo floors was noted.

Sites where nesting occurred were visited approximately every 2 wk throughout the breeding season, January–August, in 1979–1981 and 1984. During 1982 and 1983, a study to develop a sexing technique (Looman 1985) was started, and therefore we increased our efforts and visited active nest boxes more frequently (usually once a week) throughout most of the breeding season (May–August) during these years. Nests were considered active if an adult owl was observed in the nestbox or signs of recent occupation were evident (i.e., eggs, eggshells, fresh pellets in nestbox, nestlings). Onset of egg laying was determined by direct observation or by backdating from known-age nestlings or date of fledging. For backdating, we used 30 d as an incubation period (Smith et al. 1974, Marti 1992), with 2 d between individual eggs (Bunn et al. 1982). Clutch size and productivity (fledgling number) data were determined by direct observation.

Behavior of adults and nestlings was recorded at each visit. All young were banded when approximately 5–6 wk old, and during 1982 and 1983 each young was weighed at fledging (approximately 8 wk) and sexed according to the sexing method described by Looman (1985). While pellets collected during a 5-yr period (1979–1983) were available for food habit assessment, only pellets collected in 1982 and 1983 were separated into 4 time groupings, each representing a seasonal period of Barn Owl activity and roughly corresponding with 1 of the 4 seasons. The spring period (March–May) corresponded with early reproductive activities, summer (June–August) with adult attentiveness to fledgling but still dependent young. The autumn period (September–November) included abandonment and subsequent dispersal of most young, and winter (December–February) corresponded with the period that remaining owls moved into well-protected residential structures.

Pellet analysis followed Marti (1974). Vertebrate prey remains were identified by comparison with mammal (see Durrant 1952) and bird specimens at M. L. Bean Museum, Brigham Young University. Prey weights for estimation of biomass were means obtained from these specimens and from reported weight estimates (Marti 1974, Steenhof 1983). Estimated age of prey for use in biomass calculations was based on cranial features (ossification of sutures and auditory bullae and tooth eruption and wear).

Diversity of Barn Owl diet was determined using the multivariate statistical package MVSP (Kovach 1987). To allow comparisons with other published diversity indices of Barn Owl diet, diversity indices were calculated using the modified Shannon-Weiner diversity index formula

$$H = -\sum_{i=1}^{s} (p_i)(\log p_i),$$

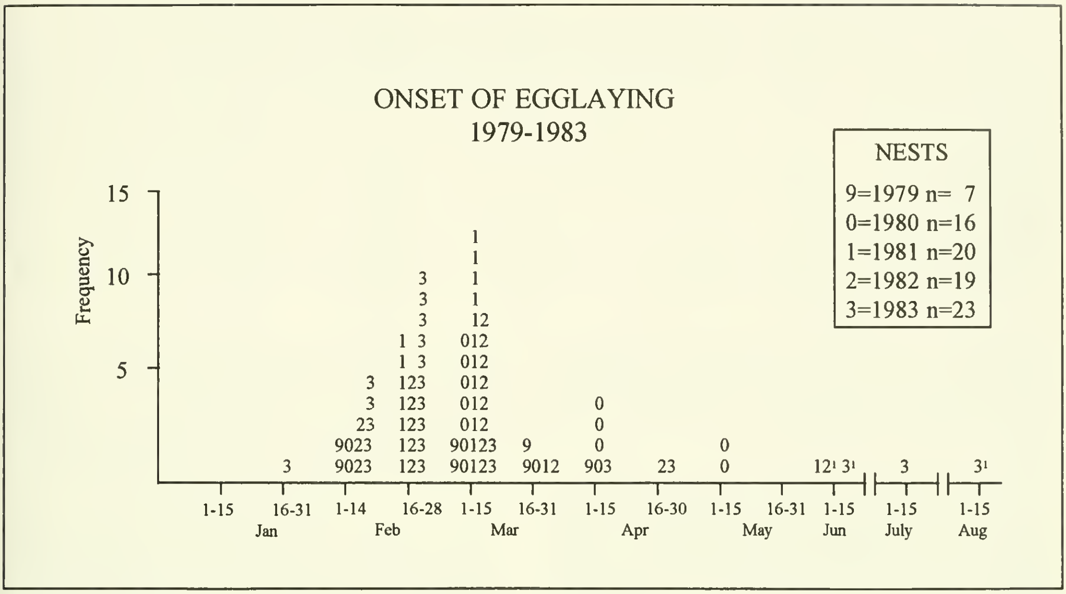
where s is the number of species and p_i is the proportion of the number of individuals in the ith species. Species evenness ($E = H/\log_2$; Magurran 1988) was also calculated.

RESULTS

Breeding Chronoloy

Dates of onset of egg laying range from early January (date obtained by backdating) through early August, with 36% commencing egg laying during the first half of March and 25% beginning in late February (Fig. 1). The earliest date on which eggs were observed in a box was February 12, the latest September 14 (eggs and nestlings observed).

Length of the nesting season for this population, defined as the period from deposition of first egg to fledging of last young, averaged 6.6 mon for the 5-yr period (range 4.0 mon in



¹Onset of second clutch

Fig. 1. Dates of first egg laying by Barn Owls in north central Utah, 1979–1983.

1979 to 9.8 mon in 1983). This is long compared to 5.3 mon in south Texas (Otteni et al. 1972) and in Utah (Smith and Marti 1976) during 1974 and 1975; no late autumn nests were found, however, as have been previously found in Utah (Smith et al. 1970). Individual nesting cycles, from deposition of first egg to fledging of last young in the nest, were approximately 3.3 (3.25 ± 0.2, $n = 10$) mon in length.

Where egg deposition intervals were known, the interval was 2 d between eggs (2.1 ± 3, $n = 10$); this is similar to deposition data (2.3 d) found for Barn Owls in Springville during 1973 (Smith et al. 1974). Known incubation times averaged 32.3 d (±3 d, $n = 10$). Fledging occurred at 62 d (±4 d), and young remained in the area until approximately 13 wk of age. Similar incubation and fledging times are reported for Barn Owls elsewhere (Pickwell 1948, Reese 1972, Smith et al. 1974).

Nests

Owls made no attempt at nest construction. However, prenesting behavior of adults, in which they spent a great deal of time at the nest site, resulted in a layer of broken down pellets, incidental feathers, and fecal material which produced a soft bed for eggs. Eggs were laid in a shallow area in the middle.

Productivity

Four hundred twenty-eight young were fledged from 104 (106 including 2nd broods) nest boxes over a 6-yr period (Table 1), averaging 3.9 young/box with a nest failure rate of 16.6%. Productivity ranged from 0.8 young fledged/box (2.0 young/active box) and a failure rate of 25% in 1979, to 4.37 young fledged/box (5.4 young/active box) and a failure rate of 9.1% in 1981.

Mean clutch size for the 5-yr period was 5.8 eggs/clutch (±1.72) and ranged from 5.3 (1979, 1983) to 6.5 (1981) (Table 2). Modal clutch size was 7 (22%); modal brood size was 7 (21%) (Table 3). Clutch size in 19 nests in 1982 ranged from 2 to 10 eggs and averaged 5.8 (±2.0); broods in these nests ranged from 2 to 7 and averaged 4.0 (±1.9) young hatched/nest. Thirty-one percent of eggs failed to hatch, and nestling mortality was approximately 8%. Productivity in 16 nests where young successfully fledged averaged 4.4 (±1.4); however, productivity fell to 3.7 (±2.1) young fledged/total nesting attempt.

Clutch size in 23 nests in 1983 ranged from 3 to 9 and averaged 5.3 (±1.8) (Table 2). Brood number ranged from 2 to 8 and averaged 3.95 (±2.1) young hatched/nest. Twenty-five percent of the eggs failed to hatch, and nestling

TABLE 1. Productivity of Barn Owls using artificial nest boxes in Juab, Utah, and Salt Lake counties, Utah, 1979–1984.

	1979	1980	1981	1982	1983	1984	Total	$\bar{x}$	s
# nest boxes surveyed	20	25	27	29	28	29	158	26.3	3.44
# boxes used as nests	8	16	22	19	23[a]	17	106	17.5	5.39
# fledged	16	63	118	71	80	80	428	71.3	33.04
# fledged/box ($\bar{x}$)	0.8	2.5	4.4	2.3	2.9	2.8	—	2.6	1.15
# fledged/used box ($\bar{x}$)	2.0	3.9	5.4	3.7	3.5	4.7	—	4.0	1.16
# unsuccessful boxes	2	4	2	2	3	2	15	2.5	.83
% unsuccessful boxes	25	25	9.1	15.8	13.0	11.8	—	15.8	7.25

[a] Single nests at which 2nd broods occurred are counted twice.

mortality was 12.5%. Nests that successfully fledged young averaged 4.0 (±1.8) fledglings, but net productivity for total attempt was 3.5 (±2.2).

Lower clutch sizes (2, 3, 4 eggs/clutch) had a relatively higher percent success than larger clutches (>4 eggs/clutch); however, clutch sizes of 8 produced the highest number of fledglings ($\bar{x} = 5.3 \pm 3.8$, $n = 3$). Clutches with 5 ($n = 8$) and 10 ($n = 1$) eggs were least productive, with approximately 50% hatching and fledging success. Seven-egg clutches were among the more productive clutch sizes, fledging an average of 5 young (±2.3), with 82% hatching success and 71% fledging success.

Three instances of 2nd broods occurred (Table 1). One female (1982) produced 7 fledglings from 1 silo and then from another silo located approximately 200 m away produced 4 fledglings from a 2nd clutch. The "alternate" nest site was consistently used for roosting throughout the previous winter and spring by a male and during the latter part of the first nesting period by the nesting pair. Since only the female of the nesting pair was banded, it is not known whether the male using the "alternate site" during winter and spring was a member of the nesting pair, or whether the same male fathered both clutches. The 2nd and 3rd instances of 2nd brood occurred in 1983. Each female produced both clutches in the same box.

Of 19 Barn Owl nesting attempts in 1982 with known outcome, 3 failed to fledge young (15.8% failure); in 1983, 3 of 23 nests failed to fledge young (13.0% failure). Nest failures were believed to have occurred during incubation or shortly after eggs hatched, judging from the lack of accumulation of fecal matter and fresh pellets. Reasons for most nest failures are unknown, but 1 case of failure was due to human disturbance (use of silo for silage storage). Other probable causes were loss of 1 or more parents or desertion, particularly in 1983, when clutches were abandoned after a long, cool, wet period following egg laying.

Although reasons for all brood reductions are unknown, some may be attributable to human disturbance, particularly where there was evidence of human activity at silos. Fratricide may have accounted for at least 2 brood reductions, where remains of young were in the nestbox or in pellets. Two reductions were investigator related and occurred when nestlings fell from the nestbox after the adult female flushed.

Sex Ratios

Of 65 fledglings sexed in 1982, 26 were males and 39 females; this is a significant overproduction of females ($\chi^2 = 2.6$, $0.5 < P < 0.10$; df = 1). However, the number of males and females produced during 1983 (of 49 fledglings sexed: 26 females, 23 males) was not significantly different from the expected 1:1 ratio.

Dispersal

Thirty-five juveniles banded in the study area between 1979 and 1983 were recovered. Of these, 61% were within 25 km of their natal site, 12% within 50 km, and the remainder within 350 km. Most recovered juveniles (54%) dispersing more than 25 km tended to fly northwest, with most live returns found occupying nestboxes in northern Utah. Twenty-three percent dispersed to the southwest.

Eleven (31%) recovered owls were less than 6 mon old; these were mostly within 1 km of the natal site and probably died while dispersing. Nineteen (54%) were approximately 1 yr old when recovered, 3 (9%) were recovered approximately 2 yr after banding, and 2 birds were 3 yr old when recovered alive. One was captured as a breeding bird at her natal site 3 yr in a row.

TABLE 2. Clutch sizes (% of yearly total) of Barn Owls in Juab, Utah, and Salt Lake counties, Utah, 1979-1983.

	1979	1980	1981	1982	1983	Total
# nests	(7)	(16)	(20)	(19)	(23)	(85)
# eggs						
1	0	0	0	0	0	0
2	0	0	1 (5)	1 (5)	0	2 (2)
3	0	1 (6)	0	1 (5)	5 (22)	7 (8)
4	2 (28.6)	1 (6)	2 (10)	3 (16)	4 (17)	12 (14)
5	2 (28.6)	3 (19)	1 (5)	4 (21)	4 (17)	14 (16)
6	2 (28.6)	5 (31)	4 (20)	2 (10)	4 (17)	17 (20)
7	1 (14)	5 (31)	5 (25)	5 (26)	3 (13)	19 (22)
8	0	1 (6)	7 (35)	1 (5)	2 (9)	11 (13)
9	0	0	0	1 (5)	1 (4)	2 (2)
10	0	0	0	1 (5)	0	1 (1)
Total eggs	37	95	130	111	121	494
Mean (*s*)	5.3 (1.13)	5.9 (1.29)	6.5 (1.67)	5.8 (2.03)	5.3 (1.81)	5.8 (1.72)

Mortality

Collision with automobiles, shooting, accidents, and severe winter weather coupled with food shortage have been cited as causes of mortality of adult Barn Owls (Henny 1969, Fleay 1972, Smith and Marti 1976). At least 12 roadkills were seen during summer and autumn 1982 in the study area, and accidental deaths occur frequently, particularly with dispersing juveniles (Smith and Marti 1976). Of 9 known accidental deaths of fledglings in 1982 and 7 in 1983, most were due to collisions with cars.

During the winter of 1981–82, at least 55 dead Barn Owls were found in north central Utah. During this same period, Marti and Wagner (1985) reported 77 dead Barn Owls in northern Utah. These birds were emaciated and death was attributed to starvation resulting from cold weather and deep snow. During the period most deaths occurred, mean temperatures were –9.7°C, 2.4° below normal. Snow cover was estimated at 20–25 cm, and this likely interfered with capture of *Microtus* spp., the Barn Owl's main prey.

Additional Observations

Adults and fledglings were not color marked; however, on 1 occasion, a banded fledgling from 1 silo was found among a same-age brood in a nearby (ca 0.75 km) silo. The fledgling was 9 wk old and was present at the nearby silo on 2 different occasions. Activity at the silo was monitored the night of the discovery, and the "foster" fledgling was observed accepting food brought by the adults. No territorial behavior was noted by adults or fledglings on this occasion. The only occurrence of territorial behavior noted during the 1982–83 period was aggressive behavior by a female Barn Owl nesting in a silo in Lehi toward an American Kestrel (*Falco sparverius*) nesting in a nearby building.

Pellet and Prey Analysis

A total of 2179 individual prey items were identified from 888 pellets and pellet fragments gathered from silo floors. An additional 44 prey items were identified from remains on silo floors (Table 4). At least 16 mammal species (94% of total prey), 11 bird species (4.8%), and 4 insect groups (0.5%) were identified. By individuals, *Microtus* spp. (ca 77%) and *Peromyscus* spp. (ca 7%) accounted for over 84% of total prey. Other important mammalian species included the western harvest mouse (*Reithrodontomys megalotis*), house mouse (*Mus musculus*), and pocket gopher (*Thomomys* spp.), although none constituted over 3% on an annual basis. The European Starling (*Sturnus vulgaris*) and Yellow-headed Blackbird (*Xanthocephalus xanthocephalus*) were the most frequently taken birds, each comprising 1% of the total prey.

Percent frequency of each class of food identified was strongly correlated with percentage biomass of the same class of food. Mammals (over 94% by number) made over 92% by biomass, while birds (over 4% by number) made over 7% by biomass. *Microtus* spp. made up a large proportion (73%) of the biomass, with *M. montanus* alone accounting for 38% of the biomass consumed (Table 5).

Seasonal comparisons of prey (Appendix 1) indicate that changes in relative abundance of prey items occurred during the study. Some

TABLE 3. Number of nestlings (% yearly total) fledged from artificial nest boxes in Juab, Utah, and Salt Lake counties, 1979–1984.

	1979	1980	1981	1982	1983	1984	Total
# nests	(6)	(12)	(20)	(16)	(20)[a]	(15)	(89)
# fledged (%)							
1	2 (33)	0	0	0	1 (5)	1 (7)	4 (4)
2	0	2 (17)	1 (5)	1 (12.6)	2 (10)	0	6 (8)
3	2 (33)	0	0	3 (19)	7 (35)	3 (20)	15 (17)
4	2 (33)	1 (8)	4 (20)	5 (31)	4 (20)	1 (7)	17 (19)
5	0	3 (25)	0	4 (25)	1 (5)	0	8 (9)
6	0	2 (17)	6 (30)	1 (6)	3 (15)	5 (33)	17 (17)
7	0	4 (33)	8 (40)	2 (13)	1 (5)	4 (27)	19 (21)
8	0	0	1 (5)	0	1 (5)	1 (7)	3 (3)
Mean (*s*)	2.7 (1.4)	5.3 (1.8)	5.9 (1.6)	4.4 (1.5)	4.0 (1.8)	5.3 (2.0)	4.8 (1.9)

[a] Counts 2nd clutches in single nests twice.

changes appeared to be seasonal, while others may be of a long-term nature. While *Microtus* was the most heavily used group throughout the collecting period, it was used much more frequently during winter and spring. *Peromyscus* spp. and *Thomomys* spp. were more frequent in pellets collected during summer and autumn months. *Sorex* spp. were present in pellets during autumn, winter, and spring but not summer.

Birds were used throughout the year but were least represented during summer. No single bird species was represented in pellets from all 4 seasons; however, the European Starling, House Sparrow (*Passer domesticus*), and Red-winged Blackbird (*Agelaius phoeniceus*) were represented in 3 seasons.

Analysis of prey diversity (Table 5) gives further characterization of the Barn Owl prey base. Prey species diversity of Barn Owls in north central Utah was 2.96; maximum diversity possible was 3.434. While this shows some variation and an ability to take locally abundant prey species, it indicates a degree of singular specialization on *Microtus* spp. Diversity of north central Utah Barn Owl's food habits is roughly similar to recorded values observed in other areas in North America and Europe (Selleck and Glading 1943, Hawbecker 1945, Evans and Emlen 1947, Uttendorfer 1952, Glue 1974, Marti 1974), but it is higher than values reported from the same area in 1976 (Smith and Marti 1976; Table 5). Evenness, the actual diversity of prey base as a percentage of maximum diversity possible, was 59%; this indicates Barn Owls were not sampling possible prey evenly, but rather were taking a higher percentage of more common species.

Food Brought to Nest

Food stockpiles were found at most nests during the incubation period. Stockpiling began slightly before deposition of the first egg and continued throughout the hatching period. Initial stockpiles were small, 2–5 prey items, but stockpile sizes increased as the season progressed. The largest stockpile consisted of 23 microtines, 3 starlings, and 16 Yellow-headed Blackbirds. Wallace (1948) reported a stockpile of 190 mammals, primarily rodents.

At least 9 prey species were recorded: 53% microtines, 28% Yellow-headed Blackbirds, 6% starlings, and 3% each of Red-winged Blackbirds and deer mice. Other species were the Brown-headed Cowbird (*Molothrus ater*, 1.5%), Black-billed Magpie (*Pica pica*, 1.5%), vagrant shrew (*Sorex vagrans*, 1%), and Norway rat (*Rattus norvegicus*, 1%).

DISCUSSION

Breeding and Productivity

It appears that variability of clutch size in Barn Owls is more closely related to factors other than latitude. The 5-yr mean clutch size (5.8 eggs/clutch) for north central Utah (Lat. 39°–40°N) reported herein was much higher than average clutch size of 4.2 eggs reported for areas of higher latitude, as well as for a breeding colony studied in the same area in 1973 (Smith et al. 1974); however, this was much lower than the 4-yr mean clutch size of 7.0 eggs reported by Marti and Wagner (1985) for northern Utah Barn Owls (Lat. 41°N). Additionally, there was a wide discrepancy between the modal clutch and brood sizes

TABLE 4. Total prey identified for Barn Owls utilizing artificial nest boxes in Juab, Utah, and Salt Lake counties, Utah, 1982–83.

Prey species	Number	Percent frequency	Total biomass	Percent total biomass
MAMMALS				
Microtus pennsylvanicus	215	9.8	8600.0	9.5
Microtus montanus	887	40.4	35480.0	38.7
Microtus longicaudus	377	15.4	15080.0	14.7
Microtus spp.	239	10.9	9560.0	10.4
Mus musculus	51	2.3	969.0	1.1
Neotoma cinerea	9	0.4	2493.0	2.7
Peromyscus maniculatus	102	4.7	2142.0	2.3
Peromyscus truei	2	0.1	42.0	<.1
Peromyscus spp.	63	2.9	1323.0	1.4
Sorex cinereus	6	0.3	30.0	<.1
Sorex obscurus	14	0.6	84.0	.1
Sorex vagrans	18	0.8	108.0	.1
Sorex spp.	28	1.3	154.0	.2
Spermophilus variegatus	1	tr.	177.0	.2
Rattus norvegicus	5	0.2	1100.0	1.2
Reithrodontomys megalotis	32	1.5	350.0	.4
Thomomys bottae	50	2.3	4250.0	4.6
Thomomys talpoides	1	tr.	85.0	.1
Mephitis mephitis	5	0.2	4110.0	4.5
Total mammalian individuals	2105	94.6	86236.0	92.4
BIRDS				
Agelaius phoeniceus	9	0.4	432.0	.5
Columba livia	1	tr.	332.0	.4
Icterus galbula	7	0.3	231.0	.2
Molothrus ater	1	tr.	41.0	<.1
Passer domesticus	8	0.4	216.0	.2
Passerculus sandwichensis	2	0.1	42.0	<.1
Pica pica	2	0.1	360.0	.4
Sturnus vulgaris	23	1.0	1817.0	2.0
Turdus migratorius	1	tr.	79.0	<.1
Tyto alba	1	tr.	525.0	.6
Xanthocephalus xanthocephalus	23	1.0	1702.0	1.8
Unidentified birds	30	1.4	1260.0	1.4
Total avian individuals	108	5.9	7037.0	7.5
Total vertebrate individuals	2213	99.5	93273.0	99.9
INVERTEBRATES				
Carabidae	2	0.1	.4	<.1
Tenebrionidae	3	0.1	1.8	<.1
Orthoptera	2	0.1	1.2	<.1
Unidentified Coleopterans	3	0.1	.6	<.1
Total invertebrate individuals	10	0.5	4.0	<.1
Total prey individuals	2223	100.0	93281.0	100.0

[a]tr = trace

reported herein (7, clutch; 7, brood) and those reported elsewhere (Bunn et al. 1982 [5, 2], Otteni et al. 1972 [5, 3]).

Lack (1949) found mean clutch size of owls to increase with latitude and abundance of rodents. Otteni et al. (1972) found that clutch size for 112 clutches in southern Texas (Lat. 28° N) averaged 4.9 and was identical to average clutch size for 68 Maryland clutches (Lat. 38°– 43°N; Henny 1969). A mean clutch size of 5.3 eggs for Barn Owls nesting in Switzerland (Lat. 46°–47°N) was also reported by Henny (1969); Glue (1974) reported an average clutch size of 4.7 in Great Britain (Lat. 50°–55°N).

Lack (1954) suggested the number of eggs laid by each species has been established to correspond with the number of young that can

TABLE 5. Diversity indices of Barn Owl predation for Utah and other areas.

Location	# prey items	# prey species Mammals	Birds	Diversity[a]	Source
Utah					
North central	2173	16	11	2.96	this study
Box Elder Co.	178	8	1	2.31	Smith and Marti 1976
Utah Co.	3004	12	12	1.45	Smith and Marti 1976
California					
Southern	933	10	13	2.19	Selleck and Glading 1943
Central	948	20	11	3.10	Hawbecker 1945
Sierras	513	8	0	1.95	Fitch 1947
Northern	739	8	6+	2.41	Evans and Emlen 1947
Colorado	4366	6	16	2.76	Marti 1974
Idaho	202	9+	1+	1.79	Roth and Powers 1979
Michigan	6815	5	13	0.98	Wallace 1948
Ohio	1060	9	5	0.98	Phillips 1951
Pennsylvania	6165	7	17	1.46	Latham 1950
Texas	2056	6+	10	3.35	Otteni et al. 1972
Chile	3417	13+	0	2.82	Herrera and Jaksic 1980
England	47865	8+	17	2.29	Glue 1974
	3546	8	0	1.60	Webster 1973
Germany	76664	51	32	2.69	Uttendorfer 1952
Spain	12351	11+	0	2.11	Herrera and Jaksic 1980

[a] Diversity calculated using Shannon-Weiner's diversity index (H'): $-\sum_{i=1}^{s} (p_i)(\log p_i)$

be successfully raised, and successful rearing is based on the amount of food available and provided to young by adults. Otteni et al. (1972) found that southern Texas Barn Owls seemed to adjust reproductive efforts to rodent population fluctuations. They produced slightly lowered mean clutch size and number of complete clutches during periods of lower rodent prey population sizes and increased the number of young raised/pair during periods of abundant rodent prey populations. Similar findings were reported in Europe by Glue (data from Bunn et al. 1982) and Baudvin (1975), whose studies indicated that variations in fledging success were entirely linked to vole numbers. Marti and Wagner (1985) reported that a winter die-off of northern Utah Barn Owls in 1981–82 resulted in a later egg-laying season, a 40% decline in breeding attempts, and a decline in average clutch size from 7.0 to 5.8 eggs; however, decline in productivity was not paralleled in our study area during this period. These findings indicate that Barn Owl productivity may be closely tied to availability of prey, and that differences between clutch and brood sizes reported herein, and those reported in the same and in different areas of the Barn Owl range are likely correlated with fluctuations in prey populations and weather as they affect prey availability.

Production of 2nd broods by Barn Owls is thought to be triggered by an abundance of prey (Honer 1963). All 3 pairs producing 2nd clutches during this study, 1 in 1982 and 2 in 1983, successfully fledged young from their 1st brood. In these cases, deposition of the 1st egg of the 2nd brood occurred several weeks after the last young of the 1st brood fledged. Second broods are often less successful than 1st broods, since prey numbers decline later in the season when hatchlings still require feeding (Bunn et al. 1982). This was not the case with our observations. All 3 second nests were successful, with 2 nests 100% successful in hatching and fledging, and 1 sustaining 60% mortality of eggs but 100% success in fledging young. Furthermore, the 3 pairs successfully fledged 27 young for the breeding season, an average of 9 young per pair.

Henny (1969) suggested that in northern environments high biotic potential of Barn Owls may serve as a "built-in compensating factor" that affords protection against low years in rodent cycles and allows rapid restoration of Barn Owl populations to previous "good rodent year" size. Second-clutching during

1982 and 1983 may be 1 response to lowered population numbers resulting from the winter die-off of 1982 and abandoned clutches resulting from cool, wet weather following egg deposition in 1983.

Food Habits

Barn Owls in Juab, Utah, and Salt Lake counties sustained themselves almost exclusively by consuming mammals and birds, despite seasonal abundance of large invertebrates, reptiles, and amphibians. Year-round presence of microtine species in the diet is in agreement with other data throughout the Barn Owl's range (Wallace 1948, Phillips 1951, Otteni et al. 1972, Smith et al. 1972, Webster 1973, Lovari 1974, Lovari et al. 1976, Smith and Marti 1976, Roth and Powers 1979, Herrera and Jaksic 1980).

Webster (1973) and Wallace (1948) noted that numbers of secondary prey species captured by Barn Owls are inversely proportional to numbers of microtines captured, particularly when Sorcidae spp. form the main alternative to Microtinae. Although *Sorex* spp. were utilized frequently by Barn Owls in north central Utah, no inverse relationship could be seen between proportions of *Sorex* spp. and *Microtus* spp. An inverse relationship was noted for proportions of *Microtus* spp. and *Peromyscus* spp. *Peromyscus* spp. were clearly the main alternative to *Microtus* spp. In studies where numbers of secondary prey species are inversely proportional to numbers of microtines, the correlation has been linked with relative proportions of woodland and open areas in the owls' territories (Bunn et al. 1982). Woodlands exist in isolated areas throughout the study area, adjacent to lakes, streams, and foothills, but open field areas are more common. Thus, during summer and autumn, one or both adults may have been foraging more frequently in woodland areas (represented by *Peromyscus* spp.) than in open field areas (represented by *Microtus* spp.). During winter and spring, foraging may have shifted more to open field habitats. Alternatively, increased occurrence or availability of *Peromyscus* spp. resulting from increased reproductive activity during summer and autumn months may account for the shift in diet.

Only a few unusual prey items are noteworthy: predation on a group of striped skunks (*Mephitis mephitis*: 2 adults, 3 juveniles) at a silo in Nephi [C. Marti (personal communication) doubts that the owl would have killed so large an animal, but the evidence found clearly indicated that owls nonetheless fed on skunks]; presence of a stockpiled rock squirrel (*Spermophilous variagatus*) and a sora (*Porzana carolina*); cannibalism indicated by presence of a juvenile Barn Owl skull among loose pellets collected in autumn, as well as the discovery of what looked like a partly consumed juvenile Barn Owl in another nestbox.

Cannibalism has been reported in California (Henny 1969) during years when food supplies were low, and Baudvin (1975) reported cannibalism as the major source of Barn Owl nestling mortality in France. Often during this study, owlets (as well as eggs) seem to have "disappeared" without a trace. These may have been cannibalized, they may have died and been moved to another site, they may have been eaten by an adult or a sibling, or they may have been predated by another species. While asynchronous hatching characteristic of Barn Owls is thought to facilitate cannibalism (O'Connor 1978), care should be taken in ascribing Barn Owl remains in pellets to cannibalism.

Sex Ratios

Mendenhall (1983) reported an equal production of sexes in captive Barn Owls at Patuxent Wildlife Research Center, Maryland, but data from the wild are few. The higher proportion of female fledglings observed in north central Utah during 1982 was significant ($\chi^2 = 2.6$, $P < 0.10$; df = 1), particularly in view of the high adult winter-kill observed during the severe winter of 1981–82, and the hypothesis of sex-biased brood reduction favoring female offspring during periods of food (or other environmental) stress (Howe 1977, Newton 1979, Bildstein 1981) is supported. While a single season's deviation from expected unity could well be stochastic, differential production of sexes during environmentally stressful periods has been observed in a number of vertebrate groups (Howe 1977, Bull 1980, Charnov 1982).

Polygynous behavior by Barn Owls (Baudvin 1975, Bunn et al. 1982, Marti 1990) should be considered when addressing the differential sex ratio. Differential sex ratios among polygynous birds are fairly well established (Newton

1979, Fiala 1981, Charnov 1982). Polygynous species tend to show differential production of sexes more frequently than monogamous species (Lack 1954, Verner 1964, Zimmerman 1966), although hypotheses regarding proximate and ultimate causes vary. Olsen and Cockburn (1991) have shown that raptors frequently have a naturally biased sex allocation toward females. The reasons for such an allocation were not clear although their data did not implicate polygyny. No verified polygynous behavior was noted during this study; however, the close association between the "foster" fledgling and parents of a separate brood reported herein indicates a possibility of shared parentage, particularly since the foster fledgling's natal site was so close. Unfortunately, adult males from either silo were never captured for banding, so pairing was unknown. An alternative explanation of the "foster" fledgling behavior is that the dispersing fledgling observed adults leaving and entering the adjacent silo, and in stereotypic behavioral fashion it followed the adults. Once near the nest, normal brood begging would have elicited feeding response from the adults.

Further information on Barn Owl mating behavior and dispersal is needed to elucidate the differential production of females observed during this study. More importantly, documentation of sex ratios, both at birth and fledging, over many years is required to place the observed skewed sex ratio into perspective.

Addendum: Since the final editing of this paper a major review of Barn Owls by Marti (1992) appeared. One should consult that paper for recent details relevent to our findings.

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(Appendix 1 begins on the following page.)

Appendix 1. Vertebrate food items taken seasonally by Barn Owls in Juab, Utah, and Salt Lake counties, Utah, 1982–83.

Season	Spring[a]		Summer[b]		Autumn[c]		Winter[d]	
	Total[e]	%[f]	Total	%	Total	%	Total	%
MAMMALS								
Mephitis mephitis	0	0	0	0	5		0	0
Microtus longicaudus	191	87	54	50	108	73	24	100
Microtus pennsylvanicus	138	75	7	33	41	64	29	67
Microtus montanus	489	100	67	100	280	100	51	100
Microtus spp.	109	—	19	—	78	—	33	—
Mus musculus	25	56	3	33	21	64	2	67
Neotoma cinerea	1	6	0	0	8	46	0	0
Peromyscus maniculatus	27	44	23	67	49	91	3	67
Peromyscus truei	0	0	0	0	2	18	0	0
Peromyscus spp.	16	—	11	—	36	—	0	—
Rattus norvegicus	4	6	0	0	1	9	0	0
Reithrodontomys megalotis	20	69	1	17	8	46	3	67
Sorex vagrans	12	44	0	0	3	18	3	67
Sorex cinereus	5	19	0	0	0	0	1	33
Sorex obscurus	14	25	0	0	0	0	0	0
Sorex spp.	22	—	0	—	3	—	3	—
Spermophilus variegatus	0	0	1	17	0	0	0	0
Thomomys bottae	6	31	6	50	38	46	0	0
Thomomys talpoides	1	6	0	0	0	0	0	0
Total mammalian individuals	1080	—	192	—	681	—	152	—
BIRDS								
Agelaius phoeniceus	5	25	1	17	3	18	0	0
Columba livia	1	6	0	0	0	0	0	0
Icterus galbula	3	19	0	0	4	27	0	0
Molothrus ater	1	6	0	0	0	0	0	0
Passer domesticus	4	6	0	0	2	18	2	67
Passerculus sandwichensis	0	0	2	17	0	0	0	0
Pica pica	2	12	0	0	0	0	0	0
Sturnus vulgaris	14	38	0	0	7	55	2	67
Turdus migratorius	0	0	0	0	1	9	0	0
Tyto alba	0	0	0	0	1	0	0	0
Xanthocephalus xanthocephalus	19	31	0	0	4	18	0	0
Unidentified birds	11	—	2	—	13	—	4	—
Total avian individuals	60	—	5	—	35	—	8	—
Total vertebrate individuals	1140		197		716		160	

[a] total pellets collected. 467; total nests surveyed: 15
[b] total pellets collected: 61; total nests surveyed: 6
[c] total pellets collected: 287; total nests surveyed: 11
[d] total pellets collected: 76; total nests surveyed. 3
[e] total individuals identified
[f] frequency of occurrence in nests surveyed

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ASTRAGALUS LAXMANNII JACQUIN (LEGUMINOSAE) IN NORTH AMERICA

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Key words: Astragalus laxmannii, *nomenclature, North America.*

In a recent article Podlech (1993) proposed lectotypes for two names that have implications in the flora of North America, i.e., *A. laxmannii* Jacquin and *A. adsurgens* Pallas. Both names have been used in the literature of American *Astragalus* in application to the one species that has been generally accepted in modern times as *A. adsurgens* sens. lat. (Barneby 1964). Podlech's typifications may be summarized:

***Astragalus laxmannii* Jacquin**, Hort. Vindob. 3: 22, Tab. 34. 1776.

Lectotypus (Podlech, Sendtnera 1: 270. 1993): "Planta culta in Horto Vindobonensi e seminibus a Laxmann e Sibiria (Samen von Pallas erhalten, siehe Pallas, Sp. Astragal. p. 39. 1800). Specimen a Jacquin missum (BM!)."

***Astragalus adsurgens* Pallas**, Sp. Astragal. 40. 1800. "Crescit hic Astragalus tantum in regionibus Trans-Baicalensibus, cum *A. Laxmanni* promiscue, frequens ad Selengam, Ononem, circa Tarei-noor, et usque in Mongoliae desertum."

Type (Podlech 1993): "Transbaicalia, ad Selengam, Pallas (BM!); Onenem circa Tareinoor, Pallas (BM!); Syntypen." "Lectotypus: ad Selengam, Pallas (BM!)."

Following examination of the proposals by Podlech, we obtained pertinent specimens on loan from The Natural History Museum (BM) in London, through the courtesy of A. R. Vickery. There are 7 pertinent sheets at BM, 6 from the Pallas herbarium and 1 from the Jacquin herbarium, none of them annotated by Podlech. The sheet from the Jacquin collection is labeled "Astragalus Laxmannii. Jack. Hort.VB." and has a notation on the back side, "Herbar. NJ Jacquin." It bears a single plant with a branched caudex, several stems, and inflorescences with withered flowers and early fruit. The plant fits well within the characterization of *A. adsurgens* var. *adsurgens* as described by Barneby (1964). It is certainly the plant chosen as lectotype by Podlech.

Among the 6 specimens from the Pallas herbarium, 2 bear the designation *Astragalus adsurgens* and the additional notation, "*laxmannii.*" The other 4 are annotated *A. laxmannii.* One of the specimens labeled *A. adsurgens* has 2 notations, 1 at the top, "ad [Tareinoor, crossed out] Selengam," and 1 below the specimen, "Specimen drawn in plate 31. Pall." This specimen (49221 BM) is the undoubted lectotype for *A. adsurgens.* It is mounted with at least 3 other fragments of the same species. Sheet 49227 (BM!), bearing a "Type Specimen" label and with the name *A. adsurgens*, is likely a paratype. One (49222 BM!) of the 4 sheets, all bearing the name *laxmannii,* also has a notation, "ad Selengam," and another, "ad Tareinoor." They are possible paratypes of *A. adsurgens* and are mounted with 2 other fragments. Sheets 49223, 49224, 49225 (all BM!) are all *A. laxmannii* (as annotated), but apparently they are nomenclaturally irrelevant.

Two infraspecific taxa have been recognized within *A. adsurgens* in the flora of North America. Their names require nomenclatural realignment within *A. laxmannii*, as follows:

***Astragalus laxmannii* var. *robustior* (Hooker) Barneby & Welsh**, comb. nov., based on *A. adsurgens* var. *robustior* Hooker, Fl. Bor.-Amer. 1: 149. 1831.

Astragalus nitidus var. *robustior* (Hooker) M.E. Jones, Contr. W. Bot. 10: 64. 1902.

Astragalus adsurgens ssp. *robustior* (Hooker) Welsh, Iowa State J. Sci. 37: 357. 1963.

***Astragalus laxmannii* var. *tananaicus* (Hulten) Barneby & Welsh**, comb. nov., based on *A. tananaicus* Hulten, Fl. Alaska & Yukon 1763. 1959, a substitute for *A. viciifolius* Hulten, Ark. Bot. 33B: 1, fig. 1. 1947 (non *A. viciaefolius* DC. 1802).

A. adsurgens var. *tananaicus* (Hulten) Barneby, Mem. New York Bot. Gard. 13: 616. 1964.

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INTERMOUNTAIN MOVEMENT BY MEXICAN SPOTTED OWLS (*STRIX OCCIDENTALIS LUCIDA*)

R. J. Gutiérrez[1,2], Mark E. Seamans[1], and M. Zachariah Peery[1]

Key words: Strix occidentalis, *Spotted Owl, dispersal.*

The Mexican Spotted Owl (*Strix occidentalis lucida*) is a threatened subspecies in the United States (USDI 1993). Both the Mexican and California (*S. o. occidentalis*) Spotted Owl subspecies are distributed as fragmented populations across their respective ranges (USDI 1993, LaHaye et al. 1994). However, it is not known whether these distributional patterns represent metapopulations or are the result of isolation events because no cases of interpopulation (i.e., intermountain) dispersal have been published. A true metapopulation structure would depend on dispersal among populations (Levins 1970, Gutiérrez and Harrison in press).

In the course of extensive banding of juvenile ($n = 95$), subadult ($n = 21$), and adult ($n = 57$) Mexican Spotted Owls in the Tularosa Mountains, New Mexico, we recorded 3 cases of owl movement among mountain ranges. We report herein the circumstances of these movements.

Our study area is in west central New Mexico in the Tularosa Mountains (Fig. 1). We attempted to capture and color mark every Spotted Owl during 1991–1995 in a 323-km^2 study area (approximately 70% of the Tularosa Mountain range) using the methods of Forsman (1983). In 1994 we established random sample quadrats to estimate owl densities in areas surrounding the Tularosa Mountains.

The following movements were recorded:

1. We banded an adult female owl on 24 May 1994. This bird was paired with an adult male. A female was heard vocalizing from this territory as late as 13 July 1994. This female was found dead near Deming, New Mexico, on 19 January 1995. The bird was autopsied by a veterinarian in Las Cruces, New Mexico, who said probable cause of death was electrocution, which was consistent with circumstances leading to the bird's discovery (i.e., found below a power pole where an electrical transformer short had occurred). Although the bird was 68 g lighter in weight when recovered than when banded, it was in good condition (i.e., no indication of starvation or poor health).

The bird was recovered approximately 187 km south southeast of its banding location (Fig. 1). Of particular interest was the fact that the bird probably crossed several mountain ranges before it entered treeless Chihauhuan desert grassland where it was recovered. The nearest suitable owl habitat (e.g., mixed-conifer or pine-oak forest [*Pinus ponderosa*/*Quercus* spp.]) was in the Animas Mountains, a straight-line distance of approximately 80 km. The mountain range nearest (approximately 20 km) the bird's final location was the Florida Mountains. The highest peak in these mountains is a prominent landmark (maximum elevation 2224 m) in the desert, but it contains no suitable owl habitat (Fig. 1).

We surveyed this bird's territory in early spring 1995. The male from 1994 was still present at the historical location, but we could not detect a female. However, by June we observed an adult female roosting with this male. Therefore, the female recovered at Deming apparently left her mate, a relatively uncommon event among territorial Spotted Owls (Gutiérrez et al. 1995).

2. In 1993 we banded a juvenile female owl that we recaptured 56 km west northwest of its natal site in 1994 on Escudilla Mountain, Arizona (Fig. 1). This mountain is part of the San Francisco Mountain Range. This female was paired at the time of capture and had no young.

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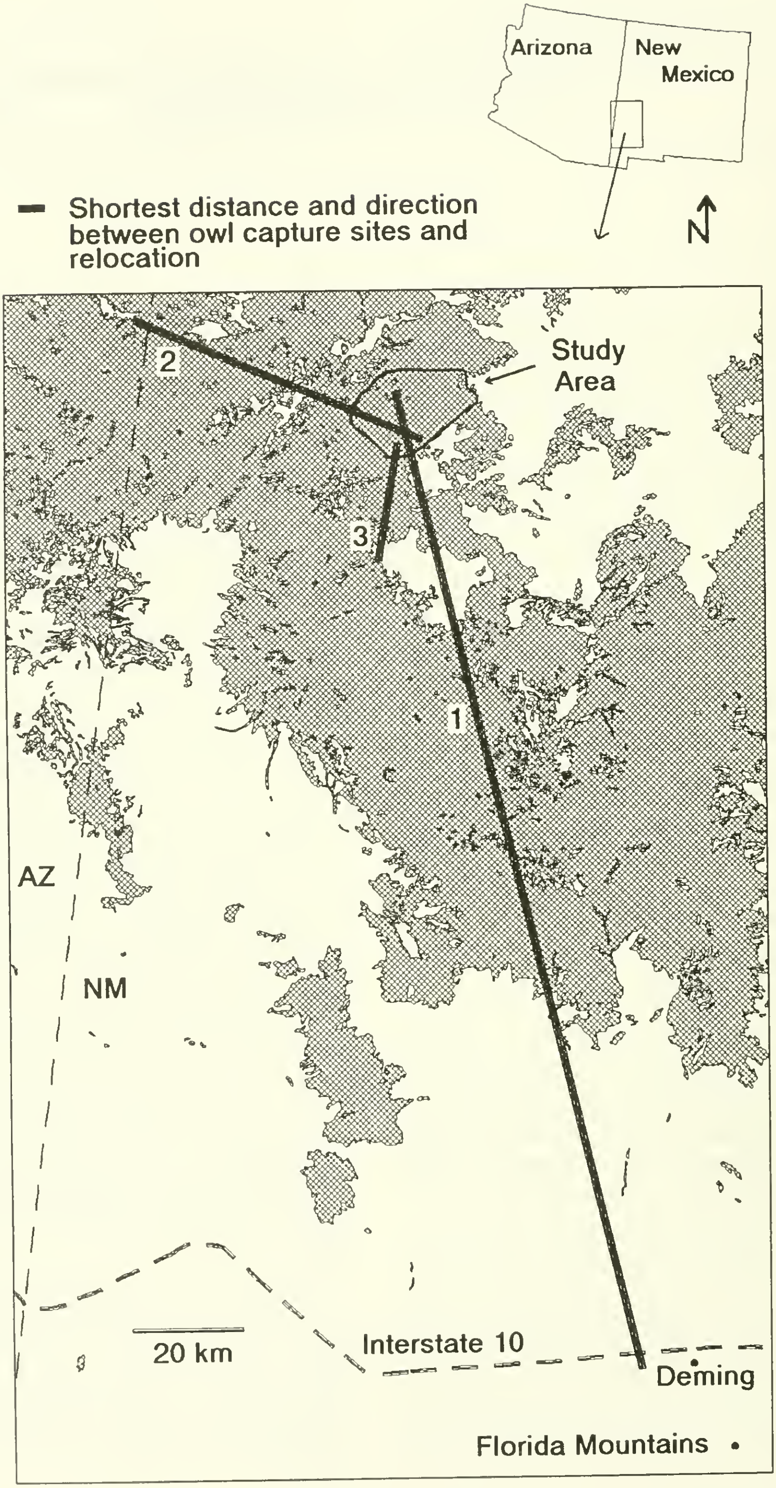
Arizona
New Mexico
Shortest distance and direction between owl capture sites and relocation
N
Study Area
1
2
3
AZ
NM
20 km
Interstate 10
Deming
Florida Mountains

Fig. 1. Shortest distance and direction between banding location and final location of dispersing Mexican Spotted Owls in New Mexico. Shaded area represents all forested/woodland areas whether or not they are suitable habitat for Spotted Owls. Numbered lines correspond to numbers in text and do not imply actual dispersal route of the bird.

3. In 1992 we banded a juvenile female owl which we recaptured in 1994 in the Mogollon Mountains, New Mexico, 22 km south of its natal site (Fig. 1). This female was paired at the time of capture and had no young.

Considering that no examples of intermountain movements have been recorded among more extensively studied California Spotted Owl populations (LaHaye et al. 1992, 1994), these observations are notable. For example, between 1987 and 1995, approximately 750 juvenile and adult California Spotted Owls were banded in the San Bernardino, San Jacinto, Palomar, and San Gabriel mountain ranges with no subsequent recoveries in another mountain range (LaHaye et al. 1994).

Our observation of female-only emigration out of the Tularosa Mountains is consistent with the general observation of female-biased dispersal in birds (Greenwood 1980). Further, during our study we relocated a total of 10 dispersing juveniles in subsequent years. Of these, 8 (5 males, 3 females) dispersed within the Tularosa Mountains. The 5 females dispersed an average of 21.8 km (range = 7.75–56.32 km, $s = 20.0$) while the 5 males dispersed an average of 5.8 km (range = 2.04–12.58, $s = 4.0$). Thus, these females dispersed farther than males (Mann-Whitney U one-tailed test, z-value = –2.194, $P = 0.0158$), which also supports the idea of female-biased dispersal in Mexican Spotted Owls.

These intermountain movements also are consistent with a metapopulation structure (Levins et al. 1970, Gutiérrez and Harrison in press). In addition, while Spotted Owls are known to be obligate dispersers (Gutiérrez et al. 1995), the long-distance movement by an adult female does not fit the general model of Spotted Owl dispersal (Gutiérrez et al. 1985) in which juveniles are the more likely long-distance dispersers. However, dispersal carries risks, such as predation, starvation, and accidents while traveling in unfamiliar habitats. Even though the adult we banded accidentally died, it is possible that adult birds, which have greater experience, may have a higher probability of success when crossing desert grasslands or otherwise unsuitable habitats in the Southwest than juveniles, who have little hunting and predator-avoidance experience. Thus, while studies of juvenile Spotted Owl dispersal are essential to the study of metapopulation dynamics (Gutiérrez and Harrison in press), the role of dispersing adults in maintaining metapopulation structure should be considered carefully.

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LIMBER PINE AND BEARS

Henry E. McCutchen[1]

Key words: limber pine, black bears, food habits, Rocky Mountains.

Limber pine (*Pinus flexilis*) is not considered a fall food for black bears (*Ursus americanus*) or grizzly bears (*Ursus arctos*) in the Rocky Mountain region of the United States. Previous studies have found that other nut-bearing plant species such as whitebark pine (*P. albicaulis*) and Gambel oak (*Quercus gambelii*) are preferred over limber pine by bears (Kendall 1983, Mace and Jonkel 1986, Beck 1991). However, these studies have been conducted only in areas where limber pine is in sympatry with other hard-mast species.

During a study of black bears from 1984 to 1992 (McCutchen 1993) in Rocky Mountain National Park, it became apparent that bears utilized limber pine some years. This paper reports on that use of limber pine and discusses the implications.

Rocky Mountain National Park, encompassing 107,000 ha, contains elevations among the highest in the continental U.S., ranging from 2440 m to 4345 m. Nearly 1/3 of the area is alpine tundra above a 3200-m timberline. Below timberline, on the upper slopes, is a subalpine zone of Englemann spruce (*Picea englemannii*) and subalpine fir (*Abies lasiocarpa*). Extensive stands of lodgepole pine (*Pinus contorta*) and scattered stands of limber pine intermixed with other species are on middle slopes. At lower elevations Douglas-fir (*Pseudotsuga menziesii*) and ponderosa pine (*Pinus ponderosa*) are common. Limber pine is not found west of the Continental Divide in the park, and the species makes up only about 1% of the forest cover (Hess 1991).

Between 1984 and 1991 I captured 40 individual black bears in and adjacent to Rocky Mountain National Park with culvert traps, with Aldrich foot snares, or at denning sites. Twenty-six bears were radiocollared (Telonics, Mesa, Arizona). Between 1984 and 1991, 9 subadult and adult bears (4 females, 5 males) were captured and radiocollared on the east side of the park. Radiolocations were primarily collected by triangulation from automobile or by hiking. I occasionally used snow tracking to determine bear activities. I used a vegetation type map (Hess 1991) to determine the proportion of radiolocations in stands containing limber pine. Bear scats were collected and analyzed at the Composition Analysis Laboratory, Fort Collins, Colorado, on a gross and microhistological scale (Sparks and Malacheck 1968).

Two female bears (2 and 3) were monitored intensively in 1985 and 1986 (McCutchen 1989). Bear 3, a 3-year-old, was captured on 6 August 1985. In 1985 bear 3 spent a significant amount of time in limber pine stands in fall. During the summer, from 6 August to 3 September, she stayed below 3047 m. We located her 11 times, and none of these locations were in limber pine. In fall, after annual plant senescence began to occur, she made a migration to near timberline and stayed above 3047 m for the next month. From 3 September to 15 October we located her 14 times; 12 of these locations were in stands containing limber pine. On 23 September and again on 11 October I tracked her in the snow and discovered that she had been feeding on nuts of limber pine cones cached in red squirrel (*Tamiasciurius hudsonicus*) middens. At each feeding site the area was littered with cone cores and scales, indicating that she spent considerable time removing nuts from cones. At 2 bed sites, 4 scats were found that consisted almost entirely of limber pine nut shells. She was radiolocated in stands containing limber pine until 15 October, when she moved and denned on 17 October.

The amount of time spent feeding in limber pine stands was high when calculated in relation to the amount of time I estimate she was

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TABLE 1. Radiofixes of black bears in and out of limber pine stands in Rocky Mountain National Park, 1985–1990.

Year	1985			1986			1987			1988			1989			1990		
Bear #	Out	In	%	Out	In	%	Out	In	%	Out	In	%	Out	In	%	Out	In	%
2	30	1	3	39	0	0	11	0	0	8	1	11	10	2	17	11	1	8
3	13	12	48	47	0	0	5	1	17	—	—	—	15	3	17	12	1	8
12	—	—	—	—	—	—	8	1	11	8	0	0	17	3	15	10	2	17
TOTAL	43	13		86	0		24	2		16	1		42	8		33	4	

out of the den during the year. Her emergence date from the den in 1985 was unknown because she had not yet been captured. However, she emerged from the den in 1986 on 9 May. Assuming she emerged in 1985 about the same time (9 May) and denned on 17 October, she was out for about 160 d. During 1985 she fed in limber pine areas from 16 September to 15 October, a period of 30 d, or 19% of her active time during the year.

Bear 2 did not utilize limber pine to the same extent as bear 3 in 1985. Although home ranges of both were adjacent (McCutchen 1989), bear 2 was located in a limber pine area only once out of 30 radiolocations. Bears 2 and 3 were again intensively radiomonitored in 1986 but were not observed to use limber pine (Table 1).

Another observation of bear use of limber pine habitat was made in 1991. A radiocollared 3-year-old male moved into bear 3's home range during emigration from his natal range about 20 km to the south. On 6 December he was tracked in the snow and was found to have dug up squirrel caches of limber pine cones and nuts. He was radiolocated in limber pine areas until 17 December.

Further analysis of radiolocations from bears on the east side of the park indicated that 4 of 9 (bears 2, 3, 12, 24) had been located in limber pine habitat at least once, 3 of these several times (Table 1). Percentage of time individual bears were found in limber pine stands varied from 0% to 48%. Of 272 total radiolocations, bears were found in forest types containing limber pine 28 times, or 10.3%.

The importance of limber pine for bears in the park during the 1985 radiotracking operation was reinforced by 14 scat samples collected during that year. Four of these (29%) consisted almost entirely of limber pine seeds.

A review of the literature on bear research north and south of the park in the Rocky Mountain region suggests that limber pine is not important if other hard-mast species are present. Black and grizzly bears fed on whitebark pine but not limber pine in Yellowstone National Park (Kendall 1983) and in northern Montana (Mace and Jonkel 1986). Aune and Kasworm (1989) found essentially no grizzly use of limber pine in 10 yr of study in the Montana Front Range. In Montana, Idaho, and most of Wyoming, whitebark pine is either the sole hard-mast species or is more common than limber pine. In south central Colorado, Beck (1991) found that black bears made long-distance movements to feed on acorns of Gambel oak but not on limber pine. However, there are areas in Colorado and Wyoming where limber pine is the sole hard-mast-producing species present and may be important to bears (Fig. 1).

Bear preference for whitebark pine and Gambel oak over limber pine is probably related to several factors. Limber pine seeds are smaller than the other two, producing 10.8 × 10^3 seeds/kg as compared to whitebark pine at 5.7 × 10^3 seeds/kg (McCaughey and Schmidt 1990) and Gambel oak at 1.3 × 10^3 /kg (Harper et al. 1985). Limber pine generally produces large seed crops at wide and irregular intervals with small amounts produced nearly every season. Whitebark pine seeds are produced at frequent and regular intervals (Harlow et al. 1979) with good crops produced at intervals of 3–5 yr (McCaughey and Schmidt 1990). In south central Colorado, Beck (1991) found Gambel oak production to be quite regular with only 1 massive acorn crop failure in 10 yr.

From the limited number of observations of limber pine use by bears in Rocky Mountain National Park, I suggest that if limber pine is the only hard mast available during certain years, perhaps years of limited production of other foods, it may be an important food source for the survival of bears. This hypothesis needs to be tested by further research.

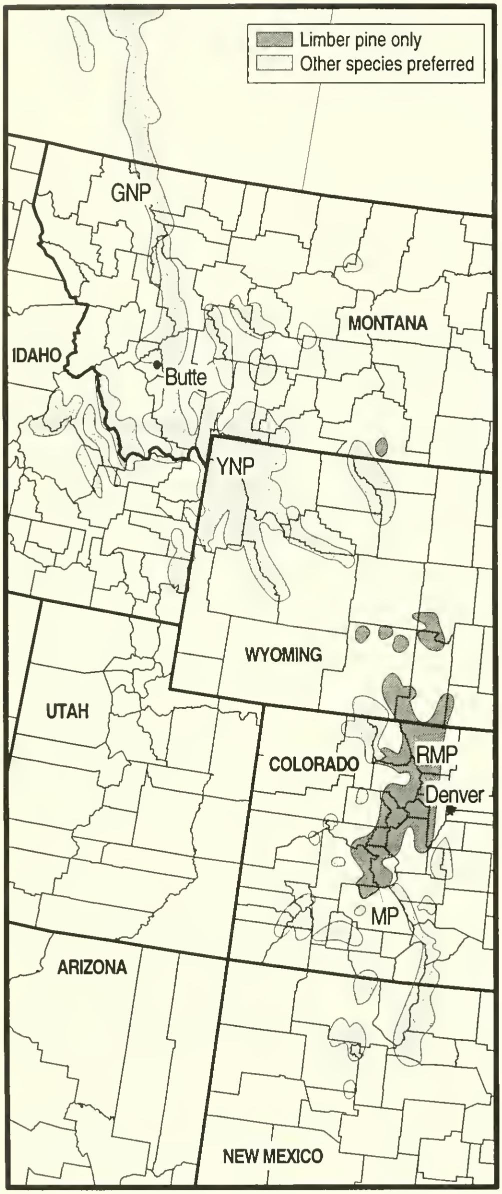

Fig. 1. Distribution map of limber pine in the Rocky Mountain region in relation to other hard-mast bear foods based on Little (1971). Limber pine only (shaded fill) designates areas where limber pine occurs exclusive of any other hard-mast species. In this area limber pine may be important to bears as a food source. Other species preferred (dotted fill) designates areas of limber pine distribution where other hard-mast species, whitebark pine to the north and Gambel oak to the south, dominate and are preferred by bears over limber pine. (Note: State and county boundaries are shown to locate limber pine range; GNP = Glacier National Park, YNP = Yellowstone National Park, RMP = Rocky Mountain National Park, MP = Monarch Pass.)

ACKNOWLEDGMENTS

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BOOK REVIEW

Utah Wildflowers: A Field Guide to Northern and Central Mountains and Valleys. Richard J. Shaw. Utah State University Press, Logan, UT. 1995. $12.95 softback.

Wildflower books belong to a genre of publications specifically designed for people who wish to see and identify pretty flowers. The wildflowers of the region covered by this handsomely designed book are certainly worthy of such a publication. It is conveniently sized for carrying into the field and presents species by flower color, as in many other books of this kind. This enables the user to find potential identities of plants encountered in the field.

As in practically all other wildflower books, the writer confronts the enigma of presenting an overall view of the plant or emphasizing the flowers alone. It is the impossibility again of having a wide-angle telephoto lens. The images are clear and sharp, and if the user is able to make the comparison of flowers alone, then the book will be very useful as an identification tool. The author of the book also had to make arbitrary decisions on which examples to treat. There are more than a thousand species of flowering plants in the region covered by this book, which treats some 92 of them. Those presented are, however, beautiful.

This book should be enjoyed for more than its usefulness in identification. It can be viewed in those times of year, and in those places, where wildflowers are not flowering. The photos will add charm and understanding by themselves.

The author and the press responsible for production of this book should be complimented.

Stanley L. Welsh
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Mack, G. D., and L. D. Flake. 1980. Habitat relationships of waterfowl broods on South Dakota stock ponds. Journal of Wildlife Management 44: 695–700.

Sousa, W. P. 1985. Disturbance and patch dynamics on rocky intertidal shores. Pages 101–124 *in* S. T. A. Pickett and P. S. White, eds., The ecology of natural disturbance and patch dynamics. Academic Press, New York.

Coulson, R. N., and J. A. Witter. 1984. Forest entomology: ecology and management. John Wiley and Sons, Inc., New York. 669 pp.

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SELECTING WILDERNESS AREAS TO CONSERVE UTAH'S BIOLOGICAL DIVERSITY

Diane W. Davidson[1], William D. Newmark[2], Jack W. Sites, Jr.[3], Dennis K. Shiozawa[3], Eric A. Rickart[2], Kimball T. Harper[4], and Robert B. Keiter[5]

ABSTRACT.—Congress is currently evaluating the wilderness status of Bureau of Land Management (BLM) public lands in Utah. Wilderness areas play many important roles, and one critical role is the conservation of biological diversity. We propose that objectives for conserving biodiversity on BLM lands in Utah be to (1) ensure the long-term population viability of native animal and plant species, (2) maintain the critical ecological and evolutionary processes upon which these species depend, and (3) preserve the full range of communities, successional stages, and environmental gradients. To achieve these objectives, wilderness areas should be selected so as to protect large, contiguous areas, augment existing protected areas, buffer wilderness areas with multiple-use public lands, interconnect existing protected areas with dispersal and movement corridors, conserve entire watersheds and elevational gradients, protect native communities from invasions of exotic species, protect sites of maximum species diversity, protect sites with rare and endemic species, and protect habitats of threatened and endangered species. We use a few comparatively well-studied taxa as examples to highlight the importance of particular BLM lands.

Key words: wilderness, biodiversity, conservation, Utah, Bureau of Land Management, endemic species, exotic species, cryptobiotic soils, plants, bees, vertebrates.

THE WILDERNESS ACT AND BIODIVERSITY

In the Wilderness Act of 1964, Congress endorsed the preservation of federal land in its natural state (16 U.S. Code, Sections 1131–36). Congress plainly anticipated that ecological considerations were an important dimension of the wilderness concept, since the act provides that wilderness may contain "ecological" features of "scientific, educational, scenic, or historical value" (16 U.S. Code, § 1131 [c][4]). Ecological concerns have also figured prominently in several congressional wilderness bills for Bureau of Land Management (BLM) public lands. Both the Alaska National Interest Lands Conservation Act, 16 U.S. Code, § 3101 (b), and the California Desert Protection Act, 103 Public Law 433 Section 2 (b) (1) (B) (1994), expressly acknowledge that wilderness designation is intended to protect important ecological

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values. Among the significant ecological functions of wilderness areas is their role in conserving biological diversity (biodiversity).

In Utah, undeveloped public lands administered by the BLM (Fig. 1) can potentially play a key role in conserving the state's natural heritage. The BLM is now pursuing an ecosystem management policy designed to ensure sustainable ecological processes and biological diversity on lands under its jurisdiction (Department of the Interior 1994). By using these same criteria to designate wilderness areas, Congress could not only advance the BLM's ecosystem management goals but also reduce conflict over the agency's multiple-use lands (e.g., by diminishing the risk of future endangered species listings and the accompanying regulatory limitations). Over the long term, it is both cheaper and easier to protect species in aggregate in their intact, functioning ecosystems than to conserve them individually in fragmented and decimated populations under the Endangered Species Act.

In short, the use of biological and ecological criteria to designate BLM wilderness areas in Utah is consistent with the legal concept of wilderness and would help to avoid future conflicts over resource management.

BIODIVERSITY DEFINED

Biological diversity—the variety of life in a given area—includes three hierarchical components: genetic diversity, species diversity, and ecosystem diversity (e.g., National Research Council 1978, Wilson 1988, Reid and Miller 1989, Raven 1992). Genetic diversity refers to the variety of genes within species. Depletion of genetic diversity during population bottlenecks, or because of inbreeding within fragmented and isolated populations, can threaten a species' survival by reducing the capacity of organisms to adapt to changing environments (Soulé and Wilcox 1980, Frankel and Soulé 1981). Species diversity, or the number of species within a region (species richness), can be divided into three major components (Whittaker 1972): alpha diversity (α), the number of species in a homogeneous habitat; beta diversity (β), the rate of species-turnover across habitats; and gamma diversity (γ), the total number of species observed in all habitats within a region. Finally, ecosystem diversity consists of the variety of major ecological communities within areas that are heterogeneous in their physical attributes, for example, in elevation or soil type.

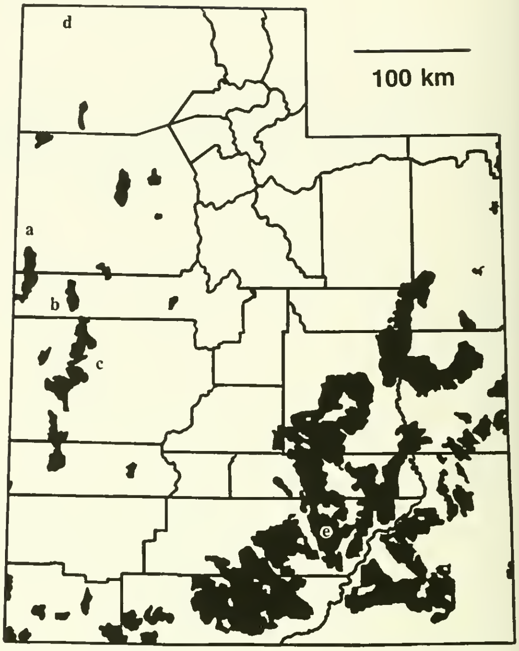

Fig. 1. Map of the state of Utah showing (in black) locations of all existing roadless areas proposed for BLM wilderness status. The BLM formally studied a subset of these areas and recommended a portion of studied lands for wilderness status. Data are from a Department of Interior map of BLM Wilderness Study Areas, BLM Proposed Wilderness, and the Utah Wilderness Coalition's BLM Wilderness Proposal. County boundaries also are shown. Isolated mountain ranges in Utah's western deserts are identified as follows: a = Deep Creek; b = Fish Springs; c = House range, and d = Newfoundland range (not formally proposed or studied for wilderness designation). On the Colorado Plateau, e = the Henry Mountains.

Genetic, species, and ecosystem diversity all result from both interactions between organisms and their environments, and interactions of organisms with one another. The physical environment sets limits on which species can inhabit an area, and interactions among those species determine which are most abundant. Strategies for preserving biodiversity must therefore take note of all living things in the landscape, and the linkages among them. Finally, since different species specialize on different stages of natural disturbance cycles, it is important to preserve a range of communities and ecosystems representing all stages in the disturbance cycle.

OBJECTIVES

The success of conserving biological diversity within a system of protected areas can only be assessed in relationship to a series of selected objectives. We propose that the conservation of Utah's biological diversity depends on (1) ensuring the long-term viability of native plant and animal populations, (2) maintaining the critical ecological and evolutionary processes upon which these species depend, and (3) protecting the full range of communities, successional stages, and environmental gradients (e.g., IUCN 1978, MacKinnon et al. 1986, Noss 1992).

Both the size of the network of protected areas and the selection of individual wilderness areas should be guided by these 3 goals. Although it is possible to preserve a small subset of species and genotypes in zoological and botanical gardens, communities and species interactions must be conserved in situ. Large areas with minimal human intrusion, and with natural processes reasonably intact, are critical elements of an in situ conservation strategy; they provide protection for fragile habitats, such as easily eroded soils, and preserve habitat for reclusive species. Moreover, wilderness areas offer natural ecosystems some protection from the biological invasions that have devastated many communities, especially plant communities, across Utah.

Here we describe a strategy, based upon widely accepted principles of conservation biology (see e.g., Primack 1993, Meffe and Carroll 1994), for both selecting critical sites for wilderness designation and determining the amount of habitat that should be preserved as wilderness (see also Babbitt 1995).

CRITERIA FOR SELECTION

Viable Populations

Utah contains approximately 3000 indigenous plant species and varieties and about 584 vertebrate species. Viable populations for most of these plants and animals can be ensured by focusing, within ecological communities, on species for which the risk of extinction is greatest. Risk-prone species typically include those with small populations, large home range requirements, low reproductive potential, restricted geographic ranges, or large temporal variation in population size (Brown 1971, Willis 1974, Terborgh and Winter 1980, Diamond 1984, Pimm et al. 1988, Belovsky et al. 1994, Newmark 1995). Many top predators have several of these traits. On BLM lands in Utah, examples of such organisms are river otter (*Lutra canadensis*) and both Bald and Golden Eagles (*Haliaeetus leucocephalus* and *Aquila chrysaetos*). Risk-prone plants include Holmgren locoweed (*Astragalus holmgreniorum*) and Jones cycladenia (*Cycladenia humilis* var. *jonesii*), which have highly specific substrate requirements.

Viability of populations depends on both the level of risk one is willing to accept, and the time frame over which one wishes to conserve the population (Shaffer 1981, Schonewald-Cox 1983, Soulé 1987). In general, both survival time and the likelihood of population persistence increase with population size. A level of risk and persistence that is commonly proposed as a management goal is a 99% chance of survival for 1000 years (e.g., Belovsky 1987, Armbruster and Lande 1993).

For large carnivores, the minimum viable population necessary to ensure a 99% chance of survival for 1000 years is estimated to be approximately 10,000–100,000 individuals (Belovsky 1987). In habitat area, this is equivalent to 100,000–1,000,000 km^2, or 2.5–25 million acres. Although this area requirement may seem remarkably large, documented losses of mammalian species from among the largest of North American national parks (e.g., the 10,328-km^2 Yellowstone–Grand Teton park assemblage) during the last 90 years make clear the importance of protecting large areas (Newmark 1987, 1995).

Maintenance of Ecological and Evolutionary Processes

In selecting wilderness areas, one must take care to ensure the maintenance of the ecological and evolutionary processes upon which all plant and animal species depend (Pickett and Thompson 1978, Kushlan 1979). Among the most important of these processes are natural disturbance and recovery cycles. Ideally, criteria for the selection of wilderness areas should include information on frequency, size, and longevity of natural disturbances. Protected areas should be large enough to contain minimum critical areas of the entire range of recovery stages for each community type (Pickett and Thompson 1978). In western North America, natural disturbance regimes can encompass tens of thousands to millions of acres, as witnessed by the recent and extensive wildfires in Yellowstone National Park (Christensen et al. 1989).

Two other critical ecological processes are migration and dispersal of terrestrial organisms across landscapes, and of aquatic species within watersheds. The selection of wilderness areas requires that attention be given to ensuring that migratory pathways are open to organisms migrating seasonally along elevational gradients. Of particular importance is the need to maintain winter ranges and migratory routes of large mammals such as mule deer (*Odocoileus hemionus*), elk (*Cervus elaphus*), and moose (*Alces alces*).

Interactions among competitors, and between predators and prey, are integral aspects of natural ecosystems and should be preserved. For example, in the southwestern deserts of the United States, the direct and indirect effects of seed predation on plant community structure have been documented in long-term experiments manipulating densities of rodent and ant granivores (Davidson et al. 1984, Samson et al. 1992). These effects include transformation of a shrubland into a grassland biome (Brown and Heske 1990). Special care must be taken to conserve populations of predators with large area requirements, because extinctions of these species can alter whole communities (e.g., by leading to outbreak densities of prey, which then overexploit their plant resources). Some of the strongest evidence for such "trophic cascades" comes from the Greater Yellowstone Ecosystem, where intensive browsing by elk has greatly altered many riparian zones by the removal of willows (genus *Salix*), and has eliminated aspen seedlings (*Populus tremuloides*) recruiting from seeds and rhizomes shortly after the extensive 1988 fires. Huge contemporary elk herds, numbering ~40,000 individuals in the park, and 20,000 in the northern herd alone, are likely the result of reductions in the full complement of large predators (Kay 1990, Wagner et al. 1995). Considerable evidence also suggests that deer and elk herds in Utah average significantly larger at present than during any extended period in the historical past (Durrant 1950, Julander 1962, Harper 1986).

STRATEGIES FOR SELECTING WILDERNESS AREAS

Landscape-wide Priorities

Given the large area requirements of many extinction-prone Utah species, it is important to protect large, contiguous land blocks. In designating wilderness areas, high priority should be given to lands whose selection would enlarge and connect existing protected areas (e.g., national parks, wildlife refuges, and Forest Service wilderness areas) and thus enhance the viability of animal and plant populations (Newmark 1985, Salwasser et al. 1987, Noss 1992, Grumbine 1994). By themselves, BLM wilderness areas in Utah clearly cannot satisfy the huge area requirements noted above as requisite for maintaining viable populations of large carnivores. However, when linked to other public lands (e.g., Utah's national parks, and wilderness areas in other states), BLM wilderness in Utah can be a key component of strategies for long-term preservation of biological diversity.

Other high-priority areas are those which, alone or together with other protected areas, encompass entire watersheds. In addition to affording direct benefits to humans, watershed protection is the most effective means of conserving the aquatic and riparian communities that account for a disproportionate fraction of both species diversity and endangered and threatened species in arid western North America (Miller 1961, Minckley and Deacon 1968, 1990, Holden et al. 1974, Johnson et al. 1977, Cross 1985, Knopf 1985, Moyle and Williams 1990). Moreover, since populations of riparian species are usually isolated from similar communities in other drainage systems, species losses from these environments are not easily remedied by natural recolonization.

A 3rd priority in selecting wilderness sites is land that forms or helps to complete the protection of entire elevational gradients, for example, in isolated mountain ranges of the Great Basin. Scant attention paid to conserving these gradients in the past is evident in the restriction of most national parks and wilderness areas in western North America to higher elevation sites. Designation of wilderness in comparatively low elevation BLM lands would afford protection to regions of greatest species richness for many organisms (e.g., mammals, birds, amphibians, insects, and trees) whose diversity generally declines with elevation throughout much of western North America (Harris 1984, Stevens 1992).

Optimal Design Goals

If BLM wilderness areas are to contribute substantially to the preservation of biodiversity in Utah, then site selection must take into account the 3 general goals outlined above. Ideally, BLM wilderness lands should form an interconnected core zone of roadless lands when combined with other federal wilderness areas, national and state parks, and wildlife refuges (Fig. 2). Special attention should be given to linking roadless lands so as to preclude further fragmentation of natural habitat. Fragmentation, or the transformation of an unbroken block of natural habitat into a number of smaller patches separated by altered habitats, reduces population sizes, increases their isolation, and threatens their long-term viability. It is one of the greatest threats to biological diversity worldwide (Wilcox and Murphy 1985, Wilcove et al. 1986, Saunders et al. 1991). Across diverse habitats, there are numerous examples of species extinctions precipitated by both natural and human-induced habitat fragmentation (e.g., Brown 1971, Terborgh and Winter 1980, Diamond 1984, Heaney 1984, Patterson 1984, Newmark 1987, 1991, 1995, Case and Cody 1988, Soulé et al. 1988, Bolger et al. 1991).

Adjacent multiple-use lands can buffer human impacts on biological diversity within wilderness areas. Such lands can be expected to provide marginal habitat for the many species that are restricted primarily to more pristine wilderness regions. Thus, proposed wilderness areas surrounded by public lands should receive high priority for protection.

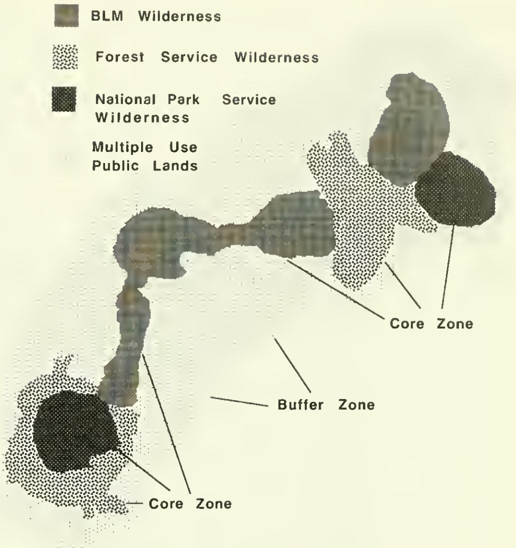
BLM Wilderness
Forest Service Wilderness
National Park Service Wilderness
Multiple Use Public Lands
Core Zone
Buffer Zone
Core Zone

Fig. 2. An example of a preferred arrangement of wilderness and multiple-use federal and state lands to conserve biological diversity. Wilderness areas administered by the Bureau of Land Management, Forest Service, National Park Service, and Fish and Wildlife Service should form a contiguous core zone in which the most extinction-prone species in Utah can be protected. Multiple-use lands can effectively buffer this core zone and provide additional marginal habitat to species that are primarily restricted to roadless areas.

EXAMPLES OF RARE AND ENDEMIC SPECIES

The design advocated above is based largely on conservation strategies for preserving wide-ranging vertebrate species. Although such strategies can help to ensure the long-term viability of most species within a given region, exclusive reliance on such approaches may well overlook and endanger many locally isolated, rare, and endemic plants and animals. We cannot give a comprehensive treatment of this subject here, but we discuss 3 taxonomic groups of organisms for which especially high rates of endemism or existing threats to isolated populations present particular management dilemmas that should be taken into account in wilderness decisions. In most cases, specific habitats must be protected to assure the preservation of these species.

Plants of Special Concern

Unlike the wide-ranging animals discussed above, plants occupy fixed positions; they and their genes move about only through the processes of seed dispersal and pollen transport. Therefore, it is not surprising that many plants have narrowly restricted ranges, are locally adapted to conditions within those ranges, and are isolated, often by great distances, from other sites where similar conditions prevail. Although locally endemic plants can often be relatively abundant inside their ranges, their populations are easily jeopardized by habitat alteration (e.g., by all-terrain vehicles) within their narrow distributions. Of Utah's approximately 2600 plant species and 400 named varieties (Albee et al. 1988, Welsh et al. 1993), about 180 (or 7% of species) are currently classified by federal or state agencies as endangered, threatened, or sensitive. A majority of these (133, or ~74%) definitely or probably occur on BLM lands (Atwood et al. 1991), and a substantial subset of the classified species are narrow endemics.

Shultz (1993) provides a useful summary of endemism in the Utah flora. Approximately 240 species, or 10% of all Utah plant species, are endemic to the state. This rate of endemism, the percentage of the flora considered for listing as threatened or endangered, and the percentage of rare species in the flora are among the highest in the continental United States. The vast majority (86%) of Utah endemics reside in arid and semiarid regions of the state, and 90% are edaphically restricted to fine-textured and/or high pH substrates (limestone, clay, silt, mudstone, and shale) that magnify drought stress. Plant distributions generally appear to respond more to edaphic, topographic, and geologic features of the environment when drought is a factor (Stebbins 1952). Because most endemics live in close proximity to morphologically similar species (Albee et al. 1988), these species appear to be mainly neoendemics that have evolved since the last glacial maximum (18,000 yrs BP), or in the Bonneville basin during the past 10,000 yrs.

Geographically, endemism of Utah plants is highest in the Canyonlands Phytogeographic Section of the Colorado Plateau Division of the Intermountain Region (Cronquist et al. 1972, Fig. 3 modified from Shultz et al. 1987). An unusual diversity of substrates occurs here, and these substrates are more apt to be exposed, rather than covered with alluvium as in other areas of semiarid Utah (Welsh et al. 1993). Thus, fully 50% of Utah's 240 rare and endemic plant species occur on the Colorado Plateau, whereas just 15% occur in the Great Basin, 11% in the Mojave Desert, and 10% in the Uinta Desert (Welsh 1978, Shultz 1993). About half of Utah's endemics belong to just 5 genera that are both common and physiologically adapted to aridity (total Utah species and percent endemics, in parentheses): *Astragalus*, Fabaceae (114, 36.8%), *Penstemon*, Scrophulariaceae (106, 26.4%), *Cryptantha*, Boraginaceae (61, 36.1%), *Eriogonum*, Polygonaceae (60, 23.3%), and *Erigeron*, Asteraceae (54, 24.1%; Welsh et al. 1975, Welsh 1978, Shultz 1993).

Because most of the state's endemic plants are restricted to particular geologic formations, and because multiple endemics often occur on the same formation, groups of endemics generally can be protected simultaneously by safeguarding those soil formations and surrounding areas. Two regions where large numbers of endemics stand to benefit from wilderness protection of BLM lands are the Uinta Basin and the San Rafael Swell and surrounding San Rafael Desert (Fig. 3, Table 1; M. Windham personal communication). No fewer than 15 plant species are endemic to the region in and around the proposed wilderness area (PWA) near the White River south of Vernal (UWC 1990), and most of these are confined to the Parachute and Evacuation Creek members of the Green River Shale formation. Another dozen endemics occur in a diversity of habitats in and around the San Rafael Swell. Here the most important habitat is a beige (rather than red) Moenkopi formation, spatially isolated from other Moenkopi outcrops and unusual in its soil chemistry. A few endemics also occur on the younger Carmel and Summerville formations surrounding the core of the swell, especially between Muddy Creek and Crack Canyon (S. Welsh personal communication). Wilderness designation in these 2 regions (the San Rafael PWA and the White River PWA of the Uinta Basin [Fig. 3]; see UWC 1990) could afford significant protection to some of Utah's endemic plants. South and east of the San Rafael, in the Dirty Devil PWA (UWC 1990), are the distinctive flora of the Orange Cliffs region (Fig. 3) and some additional narrow endemics deserving protection in the Main and South forks of Happy Canyon (Shultz et al. 1987).

The Moenkopi formation is also important as a substrate for endemics elsewhere in semiarid Utah. Two federally listed endangered species, *Arctomecon humilis* (the dwarf bearclaw poppy) and *Pediocactus sileri* (a cactus), and several other species are endemic to particular Moenkopi outcrops in southwestern Utah. Wherever possible, the boundaries of wilderness areas and other protected areas should encompass these specialized habitats.

Bees and Wasps in the San Rafael Desert

Because of their capacity for directed movements, animals are less likely than plants to exhibit high rates of endemism. Nevertheless, since insects often tend to be host- or habitat-specific (e.g., in pollinators, herbivores, or substrate-specific ground nesters), endemism can often be high in insect taxa. Bees and wasps (order Hymenoptera) are examples of such insects. Here, as elsewhere, bees and predatory wasps are especially diverse in arid regions (Michener 1979). The state supports a minimum of 950 species of native bees (roughly 25% of the total number of species known

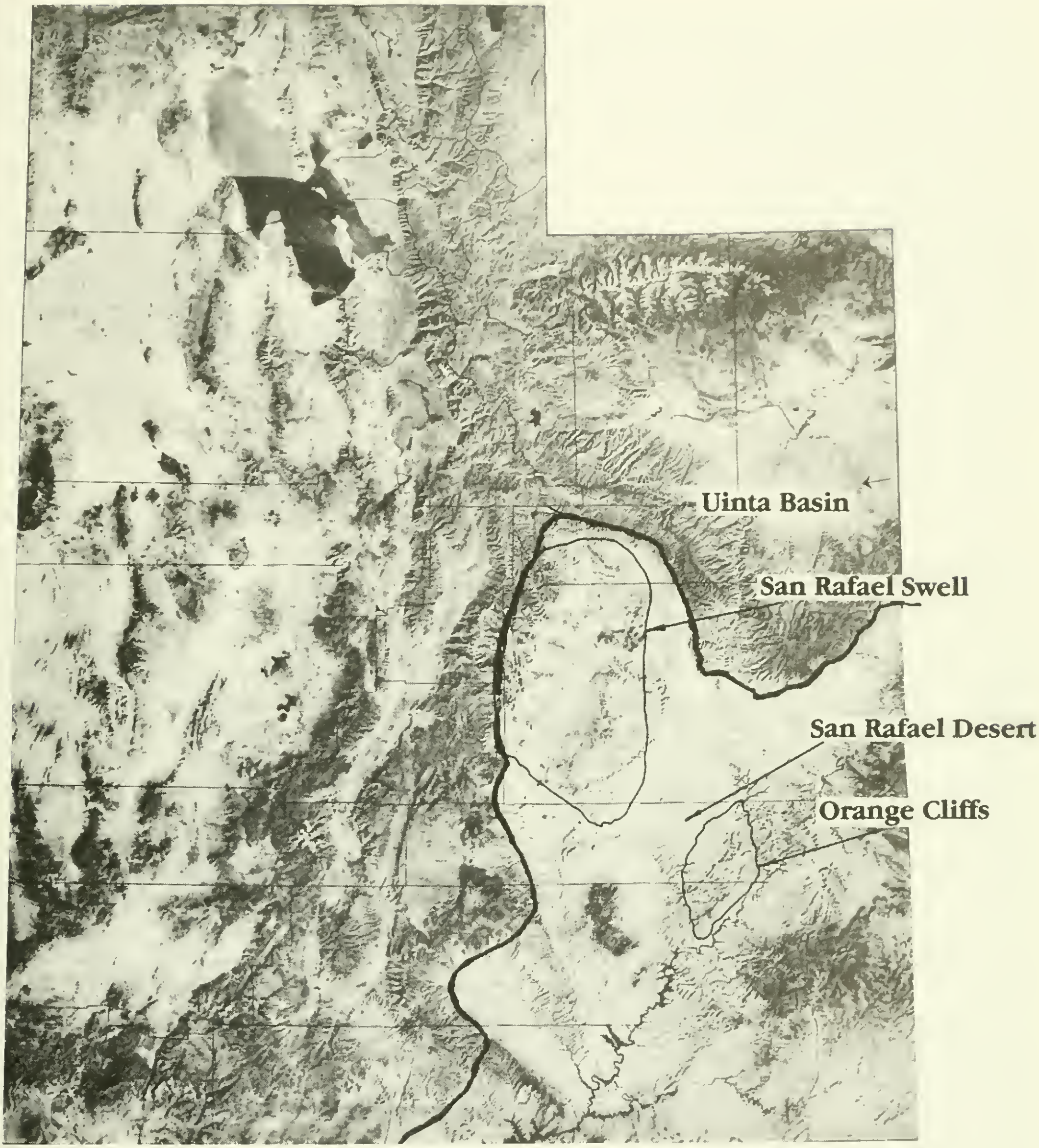

Fig. 3. Satellite image of Utah showing the positions of the San Rafael Swell, the San Rafael Desert, and the Orange Cliffs, all within the Canyonlands Phytogeographic Section, outlined in bold. The arrow in the Uinta Basin shows the approximate position of the White River PWA (Utah Wilderness Coalition 1990).

from America north of Mexico), and 50 of the Utah species are currently undescribed (T. Griswold, F. Parker, and V. Tepedino personal communication). Many areas, especially in the southern part of the state, have not been explored intensively and undoubtedly harbor many additional undescribed species.

Bees and plants often show comparable geographic patterns in diversity and endemism (Neff and Simpson 1993), and many of the areas currently under consideration for wilderness designation in Utah are centers of endemism for both groups. Although we lack extensive information on bees of the Canyonlands Section (Fig. 3), where endemism is highest for plants (see above), intensive collecting in that small part known as the San Rafael Desert has yielded a total of 316 species of bees, 42 of

TABLE 1. Plants endemic to the 2 areas with the highest endemism on Utah BLM lands.

Endemics of the southern Uinta Basin	Endemics of the San Rafael Swell
Aquilegia barnebyi Munz (Ranunculaceae)	*Astragalus rafaelensis* Jones (Fabaceae)
Astragalus equisolensis Neese & Welsh (Fabaceae)	*Cryptantha creutzfeldii* Welsh (Boraginaceae)
A. hamiltonii C. Porter	*C. johnstonii* Higgins
A. lutosus Jones	*C. jonesiana* (Payson) Payson
A. saurinus Barneby	*Erigeron maquirei* Cronquist (Asteraceae)
Cirsium barnebyi Johnst. (Asteraceae)	*Lomatium junceum* Barneby & N. Holmgren (Apiaceae)
Cryptantha barnebyi Johnst. (Boraginaceae)	*Lygodesmia entrada* Welsh & Goodrich (Asteraceae)
C. grahamii Johnst.	*Pediocactus despainii* Welsh & Goodrich (Cactaceae)
Cymopteris duchesnensis Jones (Apiaceae)	*Penstemon marcusii* (Keck) N. Holmgren (Scrophulariaceae)
Penstemon flowersii Neese & Welsh (Scrophulariaceae)	*Schoencrambe barnebyi* (Welsh & Atwood) Rollins (Brassicaceae)
P. goodrichii N. Holmgren	*Talinum thompsonii* Atwood & Welsh (Portulacaceae)
P. grahamii Keck	*Townsendia aprica* Welsh & Reveal (Asteraceae)
Schoencrambe argillacea (Welsh & Atwood) Rollins (Brassicaceae)	
S. suffrutescens (Rollins) Welsh & Chatterly	
Sclerocactus glaucus (K. Schum.) L. Benson	

which are presently undescribed (T. Griswold, F. Parker, and V. Tepedino personal communication). Thus, 33% of the state's total species count, and 84% of Utah's undescribed (but catalogued) species, are endemic to a region comprising just 2.0% of the state's land area. Furthermore, a significant portion of this fauna (24%) occurs only on the Colorado Plateau. The remainder of the Canyonlands Phytogeographic Section, in which the San Rafael Desert is embedded, is likely to be equally diverse and to have as many new species.

Other hymenopteran groups, such as the aculeate wasps, also are highly diverse in the San Rafael Desert (T. Griswold, F. Parker, and V. Tepedino personal communication). For example, with a total of 22 species there, the circumglobal genus *Philanthus* is more diverse in the San Rafael Desert than anywhere else in North America, and probably the world. These predatory "digger wasps" nest in the soil and may have diversified in response to the varied substrates present in this desert. Clearly, designation of wilderness in the San Rafael region (see UWC 1990) could afford significant protection to an area of very high endemism and diversity for the order Hymenoptera.

Bees and wasps are among the most beneficial insects. Predatory and parasitic wasps help to control populations of pest species (e.g., grasshoppers, aphids, etc.) below outbreak densities. An estimated 67% of flowering plants depend on insects (primarily bees) for pollen transfer and sexual reproduction (Axlerod 1960), and the welfare of many plant species in semiarid Utah assuredly depends on their relationships with bees. For example, a rare species of *Perdita*, found in Utah only at the BeeHive Dome site southeast of St. George, pollinates the rare and endangered dwarf bearclaw poppy (V. Tepedino personal communication). Bees that have specialized by collecting pollen only from flowers of a particular plant family, or even from a single genus within a family, are termed oligoleges. Such bees tend to be most common in arid regions (Neff and Simpson 1993) and generally are regarded as being closely adapted to the phenology and floral traits of the plants on which they specialize. Such adaptations tend to make them superior pollinators. Squash bees and squash flowers are examples of such a co-adapted pair in the Americas (Tepedino 1981). Some oligoleges may one day prove to be useful as crop pollinators. The legume specialist *Osmia sanrafaelae*, a native of the San Rafael Desert, has been investigated as a potential pollinator of alfalfa (*Medicago sativa* L.), an important forage crop (Parker 1985, 1986). Many of the species of the San Rafael Desert appear to be oligoleges. A brief list of some of the undescribed and recently described bee species and their host plants is provided in Table 2. These entries were chosen only to illustrate the variety of plant taxa upon which native bees specialize.

Native and Endemic Fishes

Freshwater ecosystems are natural habitat "islands"; as such, their long-term isolation by

TABLE 2. Pollen preferences for representative oligolectic bees in the San Rafael Desert (data from T. Griswold, F. Parker and V. Tepedino personal communication).

Plant family	Plant genus/species	Bee species
Asteraceae	*Helianthus anomolus*	*Perdita* nr. *laticincta**
		Hesperapis sp.*
	Wyethia scabra	*Perdita bohartorum*
Boraginaceae	*Coldenia*	*Perdita* (*Heteroperdita*) sp.*
	Stanleya	*Perdita* nr. *zebrata**
Euphorbiaceae	*Euphorbia parryi*	*Perdita* nr. *labergei**
Fabaceae	*Astragalus*	*Ashmeadiella* nr. *micheneri**
Loasaceae	*Mentzelia multiflora*	*Perdita multiflorae*
Onagraceae	*Camissonia*	*Dufourea* sp.*
Papaveraceae	*Argemone*	*Perdita ute*
Polemoniaceae	*Gilia*	*Perdita* nr. *giliae**
		Perdita elongaticeps
Scrophulariaceae	*Penstemon*	*Anthocopa* sp.*

*Undescribed species

intervening terrestrial habitats, or by unsuitable aquatic habitats, often promotes local specialization, evolutionary diversification, and endemism in aquatic organisms. Seven centers of endemism are recognized for fishes of western North America (Miller 1959), and Utah includes substantial portions of 2 of these centers, the Bonneville Basin and the Colorado River Basin. Collectively, 28 fish species are native to these basins (Smith 1978), and 27 are extant.

Because of their limited distributions, endemic species are easily endangered by both habitat alterations and introductions of nonnative competitors and predators. Seven species and subspecies from the Bonneville and Colorado basins are now federally listed as endangered (U.S. Fish and Wildlife Service 1993). A further 11 species and subspecies are considered by fishery specialists to be endangered, threatened, or of special concern in Utah (Warren and Burr 1994). The decline of native fishes has been associated with both watershed development (e.g., reservoirs, irrigation diversions, channelization, floodplain drainage) and the introduction of alien species.

Conservation of endemic fish populations has been especially successful when much of the watershed has been protected (Williams 1991), but adherence to strict legal definitions of wilderness often precludes such widespread protection. In Utah, opportunities for protecting entire watersheds are limited to relatively small drainage systems extending from stream headwaters in mountain ranges of the Bonneville Basin to dry or saline lake beds at lower elevations. A particularly important case is in the Deep Creek Range, where the Bonneville cutthroat trout (*Oncorhynchus clarki utah*), once thought to be extinct (Behnke 1992), survives in populations in Trout Creek and Birch Creek within the Deep Creek PWA (UWC 1990).

Where protection of whole watersheds is not possible, wilderness that includes key habitats may help to stabilize declining populations of native fishes, preclude new listings and draftings of recovery plans, and promote recoveries and delistings. This should be the case most often for fishes living in headwater streams protected by natural and artificial downstream barriers from unintended invasions of alien cold-water species. For example, habitat in the upper Book Cliffs–Desolation Canyon PWA may support the Colorado River cutthroat trout (*Oncorhynchus clarki pleuriticus*), considered the rarest of the cutthroat taxa (Behnke and Zarn 1976) and federally listed as a category 2 species (Kerchner 1995). Although the region has not been surveyed for this subspecies, native populations occur in streams entering the Duschesne River from the north (Shiozawa and Evans 1994) and have recently been found in streams of the western Book Cliffs, closer to Price and Soldier Summit (Shiozawa and Evans unpublished data). Given these observations, it is likely that streams flowing into the Book Cliffs–Desolation Canyon PWA will also contain this subspecies.

In relatively large downstream systems (secondary and tertiary streams), key habitats include floodplain wetlands, among the first habitats to be lost due to human activities. Although wetlands have been viewed traditionally either as breeding sources for insect pests or as waterfowl production sites, periodic or continuous connection to rivers renders them important appendages to lotic systems. Densities of aquatic invertebrates are significantly higher in wetlands than in main river channels, over 100-fold in some cases (Wolz and Shiozawa 1995, Mabey and Shiozawa unpublished data). Floodplain wetlands can therefore serve as important nursery grounds for larval and immature native fishes.

The loss of wetlands may be a significant factor endangering several native fishes in the Colorado River (Tyus and Karp 1989). Fishes native to the larger streams and rivers of the Colorado River Basin are predominantly minnows (Cyprinidae) and suckers (Catostomidae) that have evolved in isolation, are adapted to unique local conditions of this drainage (e.g., heavy silt loads and wide fluctuations in discharge and temperature), and are the most morphologically distinct fishes in North America (Hubbs 1940, 1941, Deacon and Minckley 1974, Minckley et al. 1986). Four of these native species, the Colorado squawfish (*Ptychocheilus lucius*), the humpback chub (*Gila cypha*), the bonytail chub (*Gila elegans*), and the razorback sucker (*Xyrauchen texanus*), are now federally listed as endangered. The decline of both the bluehead sucker (*Catostomus [Pantosteus] discobolus*) and the flannelmouth sucker (*Catostomus latipinnis*) within the main stems of the Colorado and Green rivers may result in their listings as threatened, especially if populations in tributary streams are not stabilized. Several of these species occur in areas under consideration for wilderness status. Both the Price River, in the Book Cliffs–Desolation Canyon PWA, and the San Rafael River, in the San Rafael PWA, have populations of roundtail chub, flannelmouth sucker, and bluehead sucker. Bluehead sucker are also known from the Dirty Devil and Muddy Creek drainages (Smith 1966), and both flannelmouth sucker and roundtail chub are likely to occur there. Wilderness designation could broaden the protected ranges of several of these species by stabilizing wetland habitats in the Dirty Devil, San Rafael, and Book Cliffs–Desolation Canyon PWAs.

Although the Virgin River drainage is also part of the Colorado River Basin, it has a unique fish fauna that appears to have evolved in isolation from populations in other parts of the basin. The Virgin River spinedace (*Lepidomeda mollispinus*), the woundfin (*Plagopterus argentissimus*), and the Virgin River chub (*Gila robusta seminuda*) are endemic to this system. Two additional species, the flannelmouth sucker and the desert sucker (*Catostomus clarki*), have evolved very slender caudal peduncles, possibly as a response to occasional high flows in the Virgin River (Smith 1966).

The health of this unique fish fauna already is cause for concern. Two of the endemics, the woundfin and the Virgin River chub, are federally listed as endangered. Although the desert sucker occurs in Arizona, Nevada, and New Mexico, this species merits special concern in Utah (Utah Division of Wildlife Resources [UDWR] 1992), where it is limited to the Virgin River drainage. Loss of either this species or the flannelmouth sucker from the Virgin River system would eliminate only a subset of their existing populations and is unlikely to move either species to endangered status. However, the uniqueness of these populations (Smith 1966) may warrant their designation as separate subspecies. This, together with the concern now evidenced for the flannelmouth sucker throughout its range, could easily translate into candidacy for listing if existing populations are not protected.

Concern for native fishes of the Virgin River drainage has already constrained water development in Washington County, Utah. Any actions that would help preserve the integrity of riparian habitat and stream channels would also reduce stress for these fishes. Since the integrity of riparian habitats is best maintained over large areas, wilderness designation in PWAs of the Beaver Dam slope and the greater Zion area would serve this purpose.

Finally, protection of Utah's rare and endangered fishes would likely also afford significant protection to other aquatic organisms, for example, Utah's diverse communities of aquatic insects. Reciprocally, the maintenance of high species diversity in stream insect communities is critical to assuring a continuous food supply to fishes in rivers with wide seasonal and annual fluctuations in flow rates. Mayflies (Ephemeroptera) are among the best-studied stream insects in Utah, and 16–18 genera (22–24 species) are known from warm water tributaries of the Colorado River system (G. Edmunds personal communication). Construction of reservoirs on these rivers has already inundated many river miles and altered flow rates, sediment loads, and downstream temperatures. Mayflies and other aquatic insects are highly sensitive to all these variables. Unnaturally constant temperatures in tailwaters beneath dams can lead to depauperate communities of mayflies and other stream insects, for example, below Flaming Gorge Reservoir (Edmunds 1994, 1995). (Four mayfly genera from this area of extremely high natural diversity have not been collected since the dam was built.) Habitats rich in mayflies and other aquatic insects, and most in need of protection from future impoundments, include the Green River from the Colorado border to Ouray, Utah, and the Colorado River from the Colorado border to Moab, Utah. Relatively warm sections of the Duchesne, Uintah, White, Escalante, Virgin, and Santa Clara rivers would also be sensitive to manipulations of stream flows.

EXAMPLES OF BIOLOGICALLY IMPORTANT SITES ON BLM LANDS

The floras and faunas in different parts of Utah have unique evolutionary histories determined by the geography and topography of the lands they inhabit. In this section, we discuss 4 such sites in the context of important scientific criteria (outlined above) for wilderness site selection. We also review various scientific and educational values of these same sites.

Book Cliffs and the Tavaputs Plateau

For several reasons, the Book Cliffs and Tavaputs Plateau areas, along both sides of the Green River, are critical for the long-term conservation of biological diversity in Utah. This region contains some of the largest remaining roadless areas on BLM lands in Utah (Fig. 1) and therefore provides important habitat for sensitive species with large area requirements. It includes broad elevational gradients with the potential to protect a wide range of natural communities and to maintain crucial routes for seasonal wildlife migration between high and low elevation. Furthermore, it constitutes a vital dispersal corridor linking the Uinta mountains to the north and the Colorado Plateau to the south.

Because of both the high habitat diversity and the central location of the Book Cliffs–Tavaputs region, the biota is unusually diverse and compositionally unique, and includes many species at their distributional limits. Among reptiles and amphibians, for example, the Great Basin spadefoot toad (*Scaphiopus intermontanus*), the western whiptail lizard (*Cnemidophorus tigris*), and possibly the rubber boa (*Charina bottae*) reach their eastern distributional limits here. Three additional species, the longnose leopard lizard (*Gambelia wislizenii*), the collared lizard (*Crotaphytus collaris*), and possibly the plateau striped whiptail (*Cnemidophorus velox*) are represented here by "edge" populations at the periphery of their respective ranges. Other species, such as the northern leopard frog (*Rana pipiens*), eastern fence lizard (*Sceloporus undulatus*), Great Plains ratsnake (*Elephe guttata*), and the Utah milk snake (*Lampropeltis triangulum*), have their westernmost limits in this region (Stebbins 1985, unpublished BYU museum records). While none of these species is federally listed as threatened or endangered, a few are so listed by the state (UDWR 1992). Moreover, geographically peripheral populations such as these are particularly important as dynamic foci of evolutionary change (e.g., Brown 1995, Lesica and Allendorf 1995).

The Book Cliffs–Tavaputs region also supports a rich mammalian fauna. Although our knowledge is far from complete, the area contains at least 62 native species, including a relatively stable population of black bear (*Ursus americanus*; H. Black personal communication). Recent fieldwork has resulted in records for 6 species previously unreported from the region (D. Rogers personal communication); these include Merriam's shrew (*Sorex merriami*), dwarf shrew (*S. nanus*), water shrew (*S. palustris*), big free-tailed bat (*Nyctinomops macrotis*), northern flying squirrel (*Glaucomys sabrinus*), and western jumping mouse (*Zapus princeps*). Of these species, *S. merriami*, *S. nanus*, and *N. macrotis* appear to be rare throughout their known distributions. More fieldwork is likely to produce additional records for this region.

Isolated Desert Mountain Ranges

The isolated mountain ranges in Utah's Great Basin and Colorado Deserts are extremely important biologically because of their role in maintaining critical ecological and evolutionary processes. Because of their broad elevational gradients, extending from high peaks to desert valley floors, these ranges support a wider variety of habitats and a greater diversity of species than do areas of comparable size but less elevational relief. This characteristic also enables them to support the seasonal migrations of animals ranging from large ungulates to small passerine birds. Furthermore, these mountain ranges have outstanding scientific value because they represent cool and mesic habitat islands in an otherwise warm, arid landscape. Their natural communities have developed through intermittent periods of extreme isolation (Grayson 1993). Coupled with the great geological diversity of the region, this isolation has led to the formation of unique plant assemblages, often including rare local endemics (Albee et al. 1988, Welsh et al. 1993). By illustrating how populations and communities of habitat islands are modified through colonization and extinction, these mountain ranges have played a major role in the development of theories of geographical ecology and biogeography (Brown 1971, 1995, Grayson 1993, E. Rickart in preparation).

Portions of several isolated mountain ranges are represented within PWAs on BLM lands (UWC 1990). Such ranges include the Henry Mountains of the Colorado Plateau and the Deep Creek, Fish Springs, House, and Newfoundland ranges of Utah's west deserts (Fig. 1). As the most isolated range in Utah, the Newfoundland Mountains in Box Elder County are especially distinctive. At 2129 m above sea level, Desert Peak and a considerable area of surrounding uplands would have existed as an island throughout the history of ancient Lake Bonneville. Currently, the range forms a 154+ km^2 island of arid to semiarid vegetation immersed in a salt playa sea. No doubt salt marshes have covered the present salt flats periodically as the lake has advanced or receded in response to glacial and interglacial climates. The range has therefore been an ecological island throughout nearly 2 million years of Pleistocene and Quaternary time. Given such long isolation, these mountains have much to teach scientists about the persistence, local extinction, vagility, and evolutionary dynamics of a variety of animal and plant species that either live there now or have lived there in the past. In Utah and elsewhere in the intermountain region, knowledge of these topics will be important in the future as land managers try to anticipate plant and animal responses to the increasing fragmentation and isolation of natural habitats within the human-dominated landscape (Brown 1995).

Mojave Desert in Southwestern Utah

Washington County includes Utah's only representative of the Mojave Desert, a warm desert commonly recognized by biogeographers as lying between the Great Basin Desert to the north and the Sonoran Desert to the south (Shreve 1942, Jaeger 1957, Rowlands et al. 1982, MacMahon 1986). The Mojave Desert is physically part of the Basin and Range Geological Province, but it is characterized by relatively low elevation over most of its area (600 to 1500 m above sea level) and by both limited precipitation (100–275 mm annually in most places) and warm summers (35°–40°C mean maxima for July; see MacMahon 1986). The uniqueness of the physical environment of the Mojave is reflected in its biota. Characteristic plants include the Joshua tree (*Yucca brevifolia*), creosote bush (*Larrea tridentata*), white bursage (*Ambrosia dumosa*), brittle bush (*Encelia farinosa*), and several species of saltbush (*Atriplex*). Of these, the Joshua tree can be considered endemic, and if the distribution of this species is used to define the boundaries of the Mojave Desert, then the desert covers a substantial portion of southeastern California, the southern cone of Nevada, the northwestern and west central parts of Arizona, and the extreme southwestern corner of Utah.

Judicious designation of new wilderness areas in this corner of the state could help to safeguard the many components of Utah's biological diversity that are endemic to the Mojave Desert and the associated Virgin Mountains of northwestern Arizona and adjacent Nevada. Figure 4 details land ownership in this region of Washington County. Because so much of this land is already in the public domain, there is opportunity for biodiversity conservation with minimal disruption of economic activity. Protected areas include Zion National Park, a substantial wilderness in the Pine Valley Mountains of the Dixie National Forest (no. 1 in Fig. 4), the Upper Virgin River Desert Wildlife Management Area (or DWMA, a reserve for the desert tortoise, *Gopherus agassizii*; nos. 2a and 2b in Fig. 4), the existing Beaver Dam wilderness areas that extend into Utah from Arizona (4), and the Lytle Ranch Preserve (5). Although all of these protected areas play important roles in conserving regional biodiversity, 2 of the largest areas, Zion National Park and designated Forest Service wilderness in the Pine Valley Mountains, are generally

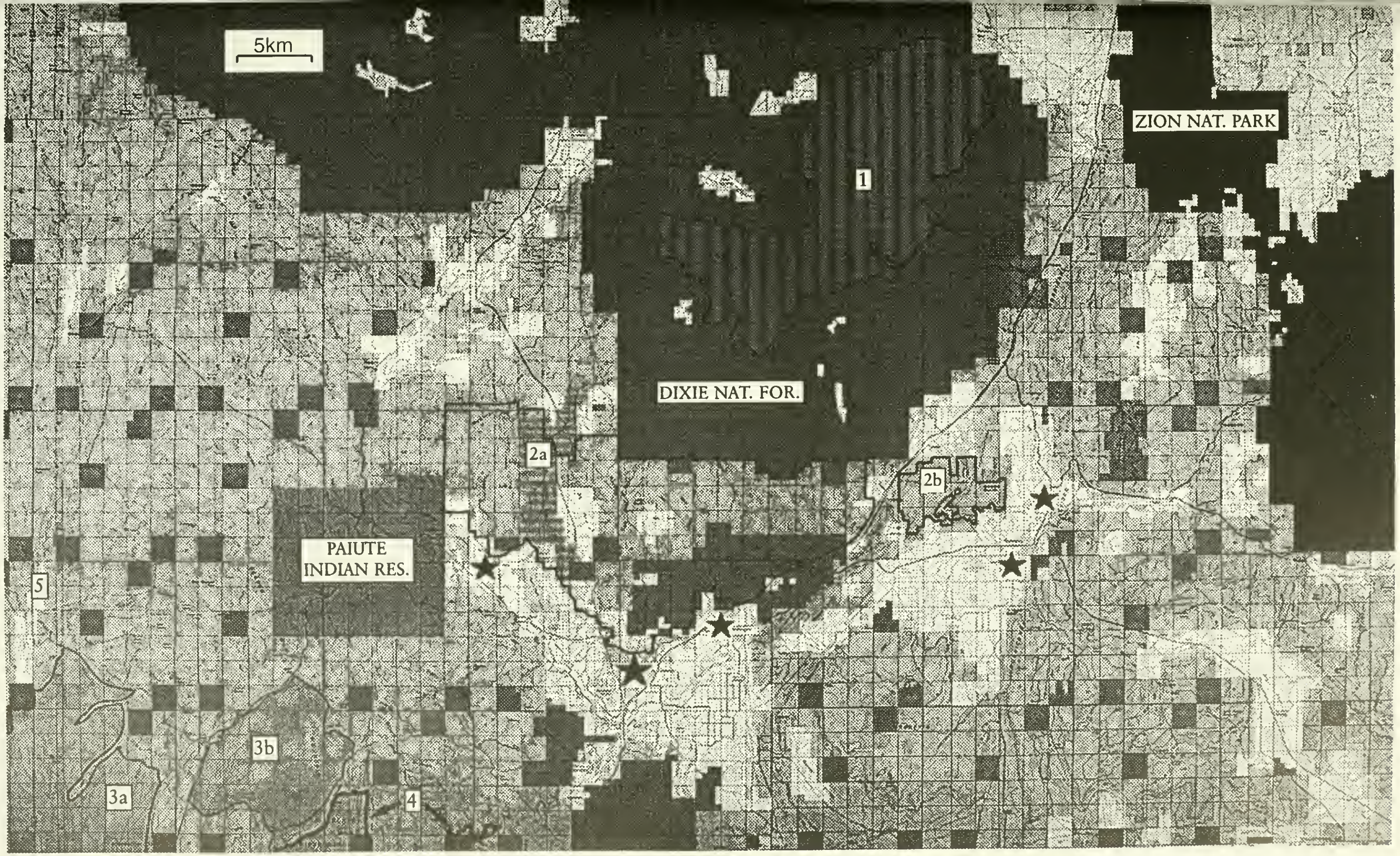

Fig. 4. Map of southwestern Utah (Washington County) showing patterns of land ownership and existing and proposed protected areas. Different shades identify privately held lands (white), BLM lands (lightest gray), and the checkerboard pattern of state lands interspersed within the BLM lands. Stars locate the major urban areas; from west to east these are Ivins, St. George (large star), Washington, Hurricane, and La Verkin. Current or proposed protected areas include Zion National Park, the Pine Valley Mountain wilderness area within the Dixie National Forest (1), Upper Virgin River DWMA (2), the proposed Beaver Dam Wash and Joshua Tree wilderness areas on BLM land (3a and 3b, respectively), the existing Beaver Dam Mountains wilderness on BLM land (4), and the Lytle Ranch Preserve (5).

too high in elevation and/or too far to the northeast to include many Mojave Desert species. The Upper Virgin River DWMA will protect lower elevation communities and will include some Mojave Desert taxa. However, many Mojave Desert species in Utah do not extend northeast of the Beaver Dam Mountains, and existing protected areas on the Beaver Dam slope are relatively small and isolated from each other (Fig. 4). By virtue of both size and location, 2 PWAs, the Beaver Dam Wash and Joshua Tree units (nos. 3a and 3b, respectively, in Fig. 4; see UWC 1990), could make important contributions to biodiversity conservation in Utah. Together these 2 units cover a range of elevations, include several distinctive plant communities not represented in the Upper Virgin River DWMA, and are close enough to one another and to the existing protected areas to serve as stepping stones for animal movement.

We illustrate the conservation value of these 2 PWAs through an example. The herpetofauna of the Mojave Desert includes 3 anurans, 1 tortoise, 16 lizards, 18 snakes, and about 28 additional species whose distributions are peripheral but extend into this desert along one of its edges (Stewart 1994). The portion of this fauna ranging into Utah includes 2 anurans, the turtle, and 13 squamates (5 lizards and 8 snakes). Their distributions across existing or proposed protected areas are summarized in Table 3. Of this total, the relict leopard frog (*Rana onca*) apparently is extinct in Utah (Platz 1984, Jennings and Hayes 1994) and therefore absent from all existing and proposed protected areas in Washington County. The other anuran confined to this part of Utah is the southwestern toad (*Bufo microscaphus*). It is known to exist with certainty in several areas and is likely widespread throughout the region where appropriate aquatic habitats exist (Table 3).

The desert tortoise (*Gopherus agassizii*) has been studied extensively over the past decade and intermittently for a much longer period of time (Woodbury and Hardy 1948, Bury and Germano 1994, Grover and DeFalco 1995). While Utah populations have apparently declined in the Beaver Dam slope area, they persist at high densities north of St. George (data summarized in Bury and Germano 1994) and are now protected in the Virgin River DWMA. Protection of the proposed Joshua Tree and Beaver Dam Wash wilderness areas would thus provide an economical way to augment conservation of tortoise populations confined to the south-facing slopes of the Beaver Dam Mountains.

Of the 13 squamate reptiles listed in Table 3, nine are confined to either the Mojave habitats proper (sites 3a, 3b, 4, and 5 in Fig. 4) or to these sites plus the Upper Virgin River DWMA (sites 2a and 2b in Fig. 4). Four species have more extensive distributions because they are also recorded from Zion National Park. Among the 9 squamates with restricted distributions, the lizards *Heloderma suspectum* and *Xantusia vigilis* and the snakes *Crotalus cerastes* and *Leptotyphlops humilis* may occur at all 5 Mojave sites, although this needs to be confirmed through additional fieldwork. *Xantusia vigilis* also occurs further east in isolated populations in Garfield and San Juan counties, and previous molecular studies by Bezy and Sites (1987) show deep genetic divisions among many isolated populations. Many of these isolates would qualify as full species, following the criteria of Davis and Nixon (1992), but the specific status of the isolated Utah populations remains unknown. The lizard *Callisaurus draconoides* occurs with certainty in the upper Virgin River DWMA (in Snow Canyon State Park), Beaver Dam Wash PWA, and Lytle Ranch Preserve (sites 2a, 3a, and 5 in Fig. 4). The iguana (*Dipsosaurus dorsalis*) is known confidently from only the lower Beaver Dam Wash PWA, although it may occur at low densities in the other 3 Mojave sites. Among the snakes, *Crotalus scutulatus* is confined to the 4 strict Mojave Desert areas, and *C. mitchellii* is known with certainty from only the higher elevation Mojave sites (3b and 4, although the other 2 locations are possible). Based on a new snake record for Utah, *Phyllorhynchus decurtatus* is known from a specimen (BYU 45605) taken on 11 July 1995, ca 1.5 mi N of the Utah-Arizona border along the Beaver Dam slope road. Based on this record, the species likely occurs in the Beaver Dam Wash and Joshua Tree areas (3a and 3b), which are similar in vegetative structure to the collecting site, and possibly at the other Mojave Desert sites as well. Regardless of exact distributions, all 9 squamate species with the most restricted distributions would benefit by wilderness designation of the proposed Beaver Dam Wash and Joshua Tree units (UWC 1990); and for 7 species (*C. draconoides*,

TABLE 3. Distribution of amphibians and reptiles restricted to southwestern Utah, relative to existing protected areas and Beaver Dam Wash and Joshua Tree units of proposed BLM wilderness included in H.R. 1500. The areas numbered are shown in Figure 4[a]. The proposed Red Mountain and Cottonwood Canyon wilderness areas (UWC 1990) are not illustrated because they are largely (Red Mountain) or entirely (Cottonwood Canyon) contained within the Upper Virgin River DWMA.

Taxon	Zion National Park	Dixie N.F. Wilderness (1)	Upper Virgin River DWMA (2A, 2B)	Beaver Dam Wash Wilderness (3A)	Joshua Tree Wilderness (3B)	Beaver Dam Wilderness (4)	Lytle Ranch (5)
ANURA							
Rana onca	—	—	—	—	—	—	—
Bufo microscaphus	+	—(?)	—(?)	+	—(?)	—(?)	+
TESTUDINES							
Gopherus agassizii	—	—	+	+	+	+	+
SQUAMATA							
Callisaurus draconoides	—	—	+	+	?	?	+
Coleonyx variegatus	+	—(?)	+	+	+(?)	+(?)	+(?)
Dipsosaurus dorsalis	—	—	—	+	?	?	?
Heloderma suspectum	—	—	+	+	?	?	+
Xantusia vigilis	—	—	+(?)	+	+	+(?)	+
Crotalus cerastes	—	—	+	+	+	+(?)	+
Crotalus mitchellii	—	—	—	?	+	+	?
Crotalus scutulatus	—	—	—	+	+	+	+
Leptotyphlops humilis	—	—	+	+	?	?	+(?)
Masticophis flagellum	+	—(?)	+	+	+	+	+
Phyllorhynchus decurtatus	—	—	—	+(?)	+(?)	+(?)	+(?)
Sonora semiannulata	+	—(?)	+(?)	+	+(?)	+(?)	+(?)
Trimorphodon biscutatus	+	—(?)	+	+	+	+	+

[a]Distributions were inferred from locality records available in research collections of California Academy of Sciences; M. L. Bean Life Sciences Museum, Brigham Young University, Provo, Utah; Museum of Vertebrate Zoology, University of California, Berkeley; Utah Museum of Natural History, University of Utah, Salt Lake City. Species listed as present (+) if they (1) exist as museum voucher specimens, (2) have been documented photographically but not collected because of threatened or endangered status, or (3) have been collected near a protected area and are known to occupy the appropriate habitat. For example, Stewart (1994) summarized distributions of all Mojave Desert amphibians and reptiles on the basis of their occurrence in distinct habitat types, and we used these data as an indication of the likely presence of a species in an area if not actually documented. Doubts about any occurrences are indicated by (?).

D. dorsalis, the 3 species of *Crotalus*, *L. humilis*, and *P. decurtatus*), these 2 PWAs would constitute the largest blocks of protected area in the Utah portions of their distributions.

The biological significance of the Mojave Desert region could be illustrated with comparable examples involving native birds, small mammals, and vascular plants; literally scores of species are restricted to the low-elevation Joshua tree habitats on the southwestern slopes of the Beaver Dam Mountains (see Behle et al. 1985, Albee et al. 1988, and Zeveloff 1988 for recent species compilations). Although most are on the periphery of their ranges, it is increasingly apparent that such peripheral populations are critical to maintaining genetic diversity and to ensuring the long-term survival of species (Furlow and Armijo-Prewitt 1995, Lesica and Allendorf 1995, Lomolino and Channell 1995). Designation of the Beaver Dam Wash and Joshua Tree PWAs as wilderness would provide an extremely economical, proactive conservation strategy for many species.

IMPACT OF ROADS ON PLANT AND ANIMAL COMMUNITIES

By definition under the 1964 Wilderness Act, wilderness areas must be large (at least 5000 acres) and roadless. Because even some remote and pristine areas contain primitive roads or tracks, roadlessness is often an issue in debates over wilderness designation. Environmentalists tend to argue that the existence of minor roads or dirt tracks is not contradictory to wilderness, but that no new roads should be built. Wilderness opponents respond that any road, no matter how primitive, disqualifies PWAs for wilderness status. Decision makers may be pressured to make exceptions to allow new roads and water development within wilderness boundaries. Here, we review the objective evidence bearing on the importance of roadlessness from a purely biological perspective. We deal with the effects of roads on animals and plants independently.

Effects of Roads on Animals

Roads affect wildlife in many ways, both direct and indirect. Among the more commonly reported adverse impacts of roads on animal populations are road mortalities, animal avoidance of roads, isolation of populations by roads acting as barriers to animal movement, reductions in natural habitats, increased poaching, and elevated erosion leading to siltation of aquatic habitats. On Utah BLM lands, large mammals such as bighorn sheep (*Ovis canadensis*), black bear, and river otter are generally intolerant of human disturbance and activities. These and other mammals are known also to avoid habitat adjacent to roads (Oxley et al. 1974, Rost and Bailey 1979, Mader 1984, Witmer and Calesta 1985, Van Dyke et al. 1986) and can therefore be displaced by the presence of roads. Historically, humans in western North America have also persecuted a number of contemporary or former occupants of BLM lands; such species include Golden and Bald Eagles, gray wolf, and grizzly bear (Bortolotti 1984, Mech 1995). In Utah, the incidence of poaching is considerably higher in regions adjacent to roads than in roadless areas (W. Woody, UDWR, personal communication).

The negative effects of roads on wildlife can generally be ameliorated by closing the roads to traffic. Road mortality and the advance of habitat alteration along roads should stop entirely, and poaching should be sharply curtailed. For larger animals, roads would likely cease to act as barriers to animal movement and gene flow. However, this might not be true for some smaller species, whose movements are more restricted generally. Significant erosion and siltation of aquatic habitats might be reduced only slightly. Siltation can be an important consideration, for example, on the Aquarius Plateau, where reductions (by as much as 1/2) in the depths of some naturally shallow lakes have already increased winter fish kills. Finally, if efforts were made to reintroduce some of the large mammals considered above, these efforts might be greatly facilitated by the protection of large blocks of roadless lands that experience minimal human intrusion.

In summary, if travel on minor roads and tracks were to be permanently restricted, most but not all of the negative effects on wildlife would likely be ameliorated. Similar reasoning would suggest that the effects of any new unpaved minor roads or tracks might be minimal if the roads were used briefly and sporadically, e.g., to carry communications equipment.

Effects of Roads on Plant Communities

The most compelling argument for large roadless areas is probably the protection of plant communities from disturbances that can eventually transform whole ecosystems. Through both direct and indirect effects, roads tend to disrupt native communities of both microphytes and macrophytes. Increased off-road vehicle traffic in roaded areas directly harms cryptobiotic soil crusts, which play a key role in maintaining healthy ecosystems in semiarid and arid lands, and kills or injures plants and perhaps soil-nesting insects like bees and wasps. Indirect effects include the introduction of nonnative pest plants, which have gradually replaced many native species and drastically altered features of certain habitats. The ecosystem-wide effects of these exotics are well illustrated by Asian tamarisk (*Tamarix chinensis*), which has channelized rivers and streams throughout the Colorado drainage and thereby altered the characteristics (flow regimes, temperatures, and sediment loads) of both aquatic and riparian habitats to the detriment of numerous native fishes, insects, birds, mammals, and plants (Loope et al. 1988, Sudbrock 1993). Below, we elaborate on the direct and indirect effects of roads on plant communities and on the maintenance of both biodiversity and natural networks of interactions in Utah's native ecosystems.

THREATS TO CRYPTOBIOTIC SOILS.—Across Utah's arid rangelands, a collection of cyanobacteria, algae, lichens, and mosses form microphytic or cryptobiotic crusts on soil surfaces. In pristine plant communities these crusts often account for at least as much soil surface cover as do vascular plants. The cryptophytes provide a number of valuable ecosystem services (reviewed in Harper and Marble 1988, West 1990, and Johansen 1993), including stabilization of soils against wind and water erosion, enhancement of water retention and infiltration (Brotherson and Rushforth 1983, Harper and St. Clair 1985, Harper and Marble 1988), and nitrogen fixation by autotrophic bacteria, including both free-living and symbiotic cyanobacteria (e.g., Snyder and Wullstein 1973, West and Skujins 1977, Klubek and Skujins 1980, Terry and Burns 1987). Their contribution to the nitrogen economy of these arid ecosystems is substantive. In southern Utah grasslands and cold deserts dominated by pinyon pine and juniper, nitrogen fixation by crusts is demonstrably the dominant source of nitrogen for vascular plants (Evans and Ehleringer 1993). The greater soil moisture and fertility associated with biotic crusts have been shown to result in higher tissue nutrient levels (Belnap and Harper 1995 and references therein), higher seedling survivorship in associated vascular plants (St. Clair et al. 1984, Harper and St. Clair 1985, Belnap 1994), and greater (α) floristic diversity (Kleiner and Harper 1972). Herbivores and other consumers may benefit indirectly from the enhanced nutrient status of these ecosystems (Harper and Pendleton 1993, Belnap and Harper 1995).

Growing recognition of the importance of cryptobiotic crusts to ecosystem processes has led to concern about the impact of disturbance by recreational users and nonnative grazers on such surfaces (Anderson et al. 1982, Johansen et al. 1984, Terry and Burns 1987, Cole 1991, Evans and Ehleringer 1993, Belnap et al. 1994, Belnap 1995). On most semiarid Utah lands, a single pass of an off-road vehicle will reduce nitrogen fixation by cyanobacteria and increase wind and water erosion of surface soils (Williams et al. 1995). Estimates of time to full recovery of disturbed biotic crusts (including nitrogen-fixing capacity) range up to 50 years in the Great Basin or 100 years on the Colorado Plateau (J. Belnap personal communication).

The full biological and economic consequences of disturbing biotic crusts remain to be quantified. However, in semiarid ecosystems where plant productivity is limited by availability of water and nitrogen, even small reductions in these resources can be expected to diminish primary productivity to the detriment of both the producers themselves and the many consumers depending directly or indirectly on these producers for food. Harper and Pendleton (1993) have suggested that destruction of soil crusts, and associated changes in forage quality, may be related to a decline in the health of desert tortoise populations in southwestern Utah (Grover and DeFalco 1995). If that suggestion is supported by empirical evidence in the future, then destruction of crusts may account in part for the ~$10 million cost (to date, T. Esque personal communication) of the Desert Tortoise Recovery Program.

ROADS AS CORRIDORS FOR INVASIONS OF INTRODUCED SPECIES.—Possibly the greatest adverse impact of roads on biological communities in Utah is the aggravation of invasions of aggressive weeds along road corridors, where disturbance from road construction has eliminated native competitors. These introduced plants now form the dominant cover on many arid and semiarid landscapes in western North America and are widespread in Utah (Mack 1981, Morrow and Stahlman 1984, Young et al. 1987, papers in McArthur et al. 1990 and Monsen and Kitchen 1994). Habitat degradation by nonnative, congregating grazers undoubtedly aided the initial spread of brome grasses (genus *Bromus*) and other European or Asian annuals into native habitats, including grasslands previously dominated by caespitose or tussock grasses (Young and Evans 1971, Loope 1976, Mack 1981, 1989, Billings 1990, 1994). Brome grasses (red brome [*B. rubens*], Japanese brome [*B. japonicus*], downy brome [*B. mollis*], ripgut brome [*B. diandrus*], and especially cheatgrass [*B. tectorum*]) have greatly increased fire frequency (from an average of 60–110 yr to <5 yr in sagebrush steppe), as well as altered the pattern and dynamics of fires (e.g., Whisenant 1990). Invaded lands suffer declining productivity (Stewart and Young 1939) and watershed damage (Buckhouse 1985) and become drastically depleted in both native plant species and cryptobiotic soil crusts (Young and Evans 1978, Whisenant 1990, Billings 1990, 1994, Rosentreter 1994; Fig. 5). Treatments to restore these lands often involve introductions of still other exotics (e.g., *Agropyron cristatum*, *Kochia prostrata*; see contributions to McArthur et al. 1990 and Monsen and Kitchen 1994).

The influx of invading weedy annuals has profound effects on genetic, species, and ecosystem diversity, although such effects remain poorly documented. In some parts of Utah,

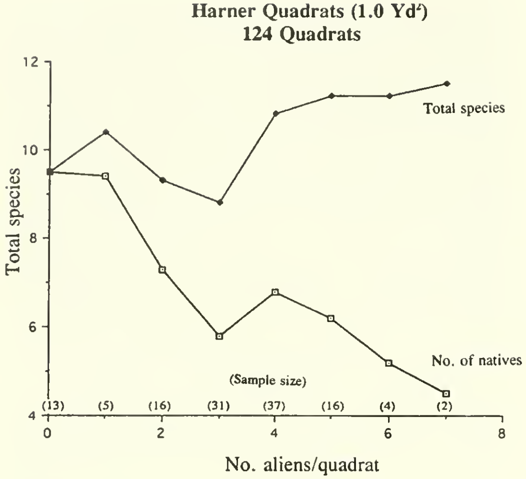

Fig. 5. Relationship of both total species richness, and numbers of native species per quadrat, to the number of individuals of introduced species per quadrat: plotted from raw data in Harner and Harper (1973). Data are from sagebrush-grasslands on private and BLM foothill lands in Salt Lake, Davis, and Tooele counties.

brome grasses form virtual monocultures, entirely replacing native communities, especially in wet years (e.g., Pellant and Hall 1994, and authors' observations). In other western states brome grass invasions threaten state or federally listed plant species (Rosentreter 1994, California Native Plant Society, personal communication). Effects of habitat conversion radiate upward through the food chain, and adverse effects have been documented on pronghorn (*Antilocapra americana*) and deer (Pellant 1990, Roberts 1994), small vertebrate prey of eagles and other raptors (Kochert and Pellant 1986, Nydegger and Smith 1986), native birds (Dobler 1994), and insects (Fielding and Brusven 1994). As summarized by Billings (1994), exotic annual grasses could constitute

> a genuine threat to the existence of large integrated ecosystems that have existed since the Pleistocene in the relatively arid lands between the Rocky Mountains and Sierra Nevada. These operational ecosystems could disappear over large areas of thousands of square kilometers.

A very high priority for future ecological work in Utah will be to determine the extent to which the remote BLM lands being considered for wilderness status might serve as refuges for native flora and fauna. Seeds of brome grass, dispersed by animal vectors, certainly travel over long distances and into wilderness areas. However, large roadless areas with low circumference-to-area ratios might protect arid and semiarid western ecosystems against wholesale habitat conversion. Exotic weeds tend to invade native plant communities mainly along roadsides, railroad right-of-ways, and other highly disturbed sites (Forcella and Harvey 1983, Hunter 1990, literature cited in Billings 1990 and 1994; see also Bergelson et al. 1993). Favorably wet drainage ditches provide inroads to new habitat, and invaders spread outward from the ditches during particularly wet years. Although systematic surveys of nonnatives do not presently exist for PWAs (and are sorely needed), there is evidence that invasions of exotic weeds may be prevented by restricting access on existing roads. Thus, of the replicate roadsides studied by Hunter (1990), introduced species (including not only brome grasses but *Erodium cicutarium*, *Salsola* spp., and *Sisymbrium altissimum*) dominated all but the one that had been closed to traffic and left undisturbed for many years prior to censusing.

The effects of roads on plant communities appear to differ importantly from those on animal communities. Construction of new roads, especially those with drainage ditches, may hasten long-term and permanent changes to local floras, and these changes may eventually have markedly adverse effects on whole ecosystems. Existing dirt tracks are probably less threatening to plant communities; although moisture conditions on the tracks may be as favorable here as in drainage ditches, soil compaction appears to retard growth of most plants.

Given the costliness of aggressive fire suppression (e.g., Vail 1994) and habitat restoration measures (see reports in McArthur et al. 1990 and Monsen and Kitchen 1994), the most economical strategy for preventing the spread of introduced grasses to areas that are still relatively pristine may be to maintain their roadless character. This also would provide opportunities for investigating the effects of roads (or lack thereof) on the advance of exotic plants on arid lands in Utah.

CONCLUSIONS

Wilderness serves many purposes, and its designation involves many and varied considerations. The technical issues and evidence presented here demonstrate that BLM wilderness lands can play a major and perhaps predominant role in safeguarding genetic, species, and ecosystem diversity across much of arid

Utah. Over the long term, large, contiguous networks of wilderness and other protected lands can provide sanctuary for populations of animals with large area requirements, and can help maintain natural processes and interactions that sustain healthy biotic communities. In many situations, wilderness designation can provide low-cost protection for rare and endangered species. BLM lands in geographically diverse regions of Utah all offer unique ecological, scientific, and educational values. To an extent so far unmeasured, wilderness lands may protect native ecosystems from wholesale transformation by invasions of exotic species. Clearly, if biological considerations are taken into account in wilderness decisions, wilderness can play a critical role in the long-term preservation of Utah's biological heritage.

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NUTRIENT DISTRIBUTION IN *QUERCUS GAMBELII* STANDS IN CENTRAL UTAH

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Abstract.—Gambel oak (*Quercus gambelii* Nutt.) is increasingly recognized as a valuable fuelwood throughout Arizona, Colorado, New Mexico, and Utah. Knowledge of the distribution of nutrients among biotic and abiotic components is an important step in developing prescriptions for managing these stands for sustainable productivity.

Eight *Q. gambelii* stands were sampled for concentrations (%) and accumulations (kg ha^{-1}) of total nitrogen (N), phosphorus (P), sulfur (S), calcium (Ca), magnesium (Mg), potassium (K), and sodium (Na) among aboveground and belowground biomass components and the upper 30 cm of soil. Highest concentrations of N, P, and S occurred in oak leaves, understory leaves, and the forest floor layer. Generally, highest concentrations of Ca, Mg, K, and Na occurred in the soil.

The greatest proportion of the total capital of individual nutrients was contained in the soil (82%–99%). Aboveground components of live biomass, standing and down-dead, and forest floor contained 10%, 14%, and 8%, respectively, of total capitals of N, P, and S. The forest floor had the largest accumulation (63%) of total nutrients (N, P, S, Ca, Mg, K, and Na) of live and dead aboveground components. Nutrient accumulation in live biomass was heavily weighted to the belowground component. The dense system of roots, rhizomes, and lignotubers comprising 56% of total biomass contained 62% of the total accumulation of nutrients in live biomass.

Low levels of total P in the soil and accumulation of 14% of the ecosystem total of P in aboveground biomass components suggest the need for a better understanding of the role of P in productivity of these stands in development of prescriptions for management of residues after harvest.

Key words: nutrient cycling, soil nutrients, nitrogen, phosphorus, sulfur, cations, Quercus gambelii, *Utah.*

Gambel oak (*Quercus gambelii* Nutt.) is found as a small shrub or large tree on about 3.8 million ha in Colorado, Arizona, New Mexico, and Utah. It is a clonal species that sprouts readily after harvest or other disturbance from a dense belowground system of lignotubers and rhizomes (Tiedemann et al. 1987). The lignotubers are similar to those found on *Eucalyptus* (Carrodus and Blake 1970). Rhizomes (belowground stems) are also common in oaks (Muller 1951).

With increasing demands for fuelwood throughout its range, *Q. gambelii* is coming under close scrutiny for its initial value as a fuelwood source and for continued fuelwood production potential (Wagstaff 1984, Clary and Tiedemann 1992). The density of the wood, its superior heat-yielding qualities compared with softwoods (Barger and Ffolliott 1972), and its sprouting nature (Tiedemann et al. 1987) make this species ideal for fuelwood management.

In the development of management strategies for sustainable productivity of *Q. gambelii*, an important step is to determine the manner in which nutrients are distributed among the abiotic and biotic components of the system. This information will help develop management guidelines so that harvest activities do not deplete nutrients to the extent that future site productivity may be jeopardized.

Our objectives were to determine the concentrations and total amounts of major plant nutrients—nitrogen (N), phosphorus (P), sulfur (S), calcium (Ca), potassium (K), magnesium (Mg), and sodium (Na)—in live and dead *Q. gambelii* biomass components and in soil, understory, and forest floor of a representative portion of the *Q. gambelii* ecosystem in central Utah; and to relate findings to similar studies in other hardwood stands. This study was a companion to a study of biomass distribution (Clary and Tiedemann 1986).

Study Areas and Methods

Eight *Q. gambelii* stands (plots) were selected near Ephraim in central Utah. The stands were on slopes with gradients from 5% to 40%. Soils are Typic Calcixerolls formed on alluvium and colluvium derived from limestone, sandstone, and shale (Swenson et al. 1981). Soils are cobbly loams in the surface 50 cm and very stony clay loams in the substratum to depths of 150 cm. Elevations of the 8 stands range from 2089 to 2480 m. Average annual precipitation ranges from 36 to 51 cm, and the annual frost-free period is 90 to 110 d (Swenson et al. 1981).

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Plot sizes varied in approximately inverse proportion to tree stem density (Clary and Tiedemann 1986). We attempted to obtain a sample of the range of stand densities and stem heights. A 3 × 3-m plot was used for the densest stand (34,444 stems/ha), a 10 × 10-m plot for the least dense stand (5000 stems/ha). Mean ages of stems ranged from 37 to 109 yr (Clary and Tiedemann 1986).

At each plot, all live stems were counted and numbered, and 5 were selected at random for measurement of height, diameter, biomass, and nutrient concentration. Sample stems were cut about 4 cm above the ground, partitioned into 60-cm sections, and weighed in the field. Live and dead branches and leaves were removed. A 10-cm portion of each bole section was placed in a plastic bag, sealed, and returned to the laboratory for determination of moisture content and nutrient concentrations. Live branches, dead branches, and leaves from each tree were bagged, returned to the laboratory, and oven-dried at 70°C to constant weight. After weighing, a sample was taken from each component for analysis of nutrient concentration. Standing dead trees were counted on each plot, and 5 were randomly selected to be cut and weighed in the field. A section was taken from each including any attached branches for determination of moisture and nutrient concentrations.

Understory biomass—including *Q. gambelii* <1 m, other shrubs, herbaceous plants, forest floor, and down and dead oak—was sampled on three 1-m^2 subplots randomly located within each plot, except plot 8, where only 1 subplot was sampled. Plot 8 was sampled at a different time from plots 1–7, with the main objective of excavation to determine characteristics of the underground system (Tiedemann et al. 1987). We inadvertently collected only 1 subplot for determination of understory biomass, forest floor, down and dead oak, and soil. On all subplots, forest floor was collected to mineral soil. No separation into litter (L), fermentation (F), and humus (H) layers was made. Hence, the forest floor includes plant detritus accumulated above mineral soil including down and dead oak <0.5 cm. All samples were oven-dried at 70°C and weighed to determine mass per unit area (kg ha^{-1}) of the forest floor. Weight of down and dead oak >0.5 cm was assigned to the category of down and dead oak trees. A small sample of each component from each 1-m^2 plot was used for nutrient analysis. Forest floor samples contained some soil as a result of wind deposition and the fact that sampling results in collection of a small amount of soil from the forest floor/soil interface. Therefore, weights of forest floor samples were adjusted for content of soil by determining weight loss on combustion of small samples in a muffle furnace at 900°C. Combustion of organic materials results in a small amount of mineral ash residue of 5 g per 100 g of forest floor (Tiedemann 1987b). We adjusted forest floor weights by this amount.

Soil volume weight (bulk density) was determined by collecting a 15- to 20-cm-diameter sample to a depth of 30 cm at each of the subplots after vegetation was harvested and the forest floor sampled. This was the maximum depth feasible to collect without using mechanized digging apparatus because of the increased rocks, cobbles, roots, and rhizomes at greater depths. The soil hole was lined with plastic and the volume determined by measuring the quantity of water to the nearest 10 mL required to fill the hole. Soil was oven-dried at 70°C, weighed, and retained for nutrient analysis. This method of bulk density determination compares favorably with the paraffin clod technique (Howard and Singer 1981).

One plot (plot 8) was hydraulically excavated to a depth of 1 m by use of a hydraulic pump capable of supplying 114 L/min (Tiedemann et al. 1987). All roots, rhizomes, and lignotubers were removed and transported to the laboratory for drying, dissecting, weighing, and nutrient analysis. Weight of roots at depths >1 m was estimated from taper-weight relationships established for the first 1 m of vertical roots. A composite sample of the roots (<1.0 cm, 1.0–2.5 cm, and >2.5 cm) and rhizomes was taken for nutrient analysis. The proportion of each component in the sample was weighted on the basis of its proportion of total weight.

Each 10-cm bole portion was separated into 8 equal radial segments. One of these from each portion was further separated into heartwood, sapwood, and bark. Samples from each radial segment were then composited for each tree prior to analysis. All vegetation samples were ground to 0.25-mm fineness in preparation for analysis of nutrient concentration. Soil samples were sieved through a 2-mm mesh screen and ground to 0.125-mm fineness prior to analysis.

All samples were analyzed for total N by Kjeldahl digestion followed by titrimetric determination of distilled ammonium (Bremner 1965); for total P by sulfuric acid–selenium digestion (Parkinson and Allen 1975) followed by molybdenum blue determination of P (Olsen and Dean 1965); for total S by the procedure of Tiedemann and Anderson (1971); and for total cations Ca, Mg, Na, and K by atomic absorption spectroscopy (Jones and Isaac 1969) on the sulfuric acid–selenium digest used for total P.

Mass per unit area (kg ha^{-1}) of individual plot values for each individual biomass component of trees (leaves, live branches, standing dead, etc.) from the study of Clary and Tiedemann (1986) were used to convert concentrations of individual nutrients to mass per unit area (kg ha^{-1}). In the biomass determination (Clary and Tiedemann 1986), stems were not partitioned into bark, heartwood, and sapwood. We determined the percentage by weight of these 3 components for each bole and converted weights to kg ha^{-1} for each plot using values from Clary and Tiedemann (1986). These values were then multiplied by concentrations of individual nutrients for determination of mass per unit area (kg ha^{-1}) content of nutrients. Mass per unit area (kg ha^{-1}) values for understory vegetation, down-dead oak, and the forest floor were multiplied by concentration values for individual nutrients to determine mass per unit area of each nutrient. Bulk density of the upper 30 cm of soil (minus particles >2 mm) was used to develop mass per unit area (kg ha^{-1}) values for soil so we could convert nutrient concentration values to mass of individual nutrients per hectare. Mass per unit area values of *Quercus* roots, rhizomes, and lignotubers in the upper 1 m of the excavated plot plus the extrapolation of larger (>2.5 cm) vertical roots to their extinction point was used to convert concentration values of nutrients to a kg ha^{-1} basis. Extrapolation was based on application of taper-weight relationships for each root.

For purposes of data presentation, nutrient contents (kg ha^{-1}) of individual aboveground biomass components were grouped into three categories: (1) aboveground live overstory and understory vegetation; (2) standing and down-dead that includes standing dead trees, dead branches on live trees, down and dead trees, and dead branches on the ground >0.5 cm; and (3) the forest floor that includes all plant detritus above mineral soil except for *Quercus* branches >0.5 cm.

Analysis of variance in a randomized complete block design with the 8 individual plots as blocks was used to determine differences in concentration among aboveground biomass components for each nutrient constituent (Steel and Torrie 1960). Biomass component was the main effect term in the analysis. Values for the 5 individual trees and for the 3 forest floor and understory subplots in each of the 8 plots (blocks) were pooled, and the means were used in the analysis of variance. Statistical comparison with underground biomass components was not possible because this was determined on only 1 plot. Where the F-test was significant, differences among individual biomass components were determined using the LSD test (Carmer and Swanson 1971). Significant differences are expressed at $P < 0.01$. No statistical tests were applied to kg ha^{-1} nutrient content data because individual components were summed to provide more inclusive groupings. For example, live aboveground biomass includes oak leaves, live branches, heartwood, sapwood, bark, and understory leaves and stems.

RESULTS AND DISCUSSION

Nutrient Concentrations

There were no significant differences in concentrations of nutrients in biomass ($P < 0.01$) among plots (blocks) for any nutrient constituent except Ca. Differences among biomass components were highly significant for every nutrient constituent.

Nitrogen concentrations in the forest floor and in *Quercus* leaves were significantly higher than in any other component (Table 1). Understory leaves were significantly lower in N concentration than the forest floor or *Quercus*

TABLE 1. Concentration (percent) of nutrient constituents in biotic and abiotic components of *Quercus gambelii*

Nutrient	Leaves	Live branches	Heartwood	Sapwood	Bark	Dead branches	Standing dead trees
N	1.57	0.56	0.15	0.27	0.62	0.55	0.35
LSD 0.01 =	0.08						
P	0.21	0.03	0.003	0.02	0.02	0.02	0.01
LSD 0.01 =	0.024						
S	0.08	0.03	0.03	0.02	0.04	0.04	0.04
LSD 0.01 =	0.014						
Ca	0.91	0.90	0.17	0.17	1.55	0.98	1.00
LSD 0.01 =	0.30						
Mg	0.35	0.16	0.02	0.04	0.20	0.14	0.08
LSD 0.01 =	0.29						
K	0.68	0.36	0.33	0.15	0.32	0.26	0.21
LSD 0.01 =	0.18						
Na	0.04	0.01	0.01	0.002	0.01	0.01	0.01
LSD 0.01 =	0.007						

[a] Comparisons among aboveground biomass components only.

leaves. We did not observe increases in N concentration of the forest floor that usually accompany decomposition, mineralization, and leaching of other constituents from the fallen overstory leaves (Bocock 1963, Gosz et al. 1973). In a litter bag study, Klemmedson (1992) measured a 60% increase in N concentration in *Q. gambelii* leaves in the litter layer over a 750-d time span. Differences between our observations and those of Klemmedson were probably because we report comparisons between *Quercus* leaves and the entire forest floor, whereas his comparisons were for the litter layer only. Lowest concentrations of N were observed in the heartwood. Standing dead and down-dead trees were both higher in N concentrations than were heartwood and sapwood of living stems. This probably resulted from selective decomposition and loss of other elements causing an increase in the concentration of N in standing dead and down-dead trees.

Concentration of N in the upper 30 cm of soil (0.42) was greater than would be expected for this site. According to Jenny (1941), the normal range of soil N for semiarid sites is 0.10%–0.25% for the surface 10 cm. The high content of N in these soils can probably be attributed to 2 principal factors: (1) the high clay content is conducive to retention of high levels of organic N (Klemmedson and Jenny 1966, Millar et al. 1966); and (2) the extraordinary accumulation of forest floor (37,348 kg ha^{-1}) at this site (Clary and Tiedemann 1986) provides a continuous supply of N to the soil through decomposition and leaching.

Leaves of understory plants (0.27%), *Quercus* leaves (0.21%), and forest floor (0.12%) had highest concentrations of P. Differences among these 3 components were significant. Reduced concentration of P in the forest floor compared to *Quercus* leaves corresponded to observations of Klemmedson (1992). Concentration of P in *Q. gambelii* leaves at the surface of the forest floor began to decrease shortly after deposit and declined steadily for 500 d to about 60% of original concentration. Concentration then leveled off for the remaining 250 d of the experiment. Our lowest levels of P occurred in the heartwood (0.003%). Although there were some significant differences among other biomass components, the actual differences were slight and probably of little biological significance. Total P in soil (0.02%) was substantially below normal levels, which are 0.09%–0.13% for soils of the United States (Parker et al. 1946).

Concentrations of S were greatest in forest floor (0.12%) and understory leaves (0.11%), and there was no significant difference between these 2 components. However, S concentration in both was significantly higher than in *Quercus* leaves. Lowest S concentrations in aboveground components were in the sapwood and heartwood. Our comparisons of N and S ecosystems in cental Utah.[a]

Understory leaves	Understory stems	Down-dead trees	Forest floor	Roots and rhizomes	Lignotubers	Soil
1.46	0.54	0.43	1.66	0.44	0.33	0.42
0.27	0.05	0.01	0.12	0.03	0.02	0.02
0.11	0.04	0.06	0.12	0.04	0.03	0.04
0.98	0.61	0.76	2.67	0.97	1.15	1.29
0.40	0.17	0.11	1.15	0.14	0.09	1.92
1.14	0.64	0.07	0.43	0.21	0.14	0.87
0.008	0.02	0.005	0.06	0.02	0.008	0.08

levels in the forest floor with *Quercus* leaves presented an anomaly. We would expect S comparisons between forest floor and *Quercus* leaves to be similar to those for N, because S is a companion to N in several amino acids (Allaway and Thompson 1966, Coleman 1966). Klemmedson's (1992) observations bear this out because both N and S concentrations in *Quercus* leaves increased about 60% over a 750-d period after deposition at the surface of the forest floor. However, when we compared *Quercus* leaves and the entire forest floor, it appeared that N and S responded differently over the long periods required for development of the forest floor. Nitrogen concentration tended to remain constant and S concentration increased over time. Mineralization of S in deeper layers of the forest floor may proceed more slowly than mineralization of N, thereby resulting in an increase in S concentration. Products of decomposition for N may also be more mobile than those for S.

Total S concentration in soil (0.04%) was in the middle of the range reported for U.S. soils, 0.01–0.06 (Burns 1968). The ratio of N:S of 10:1 in soil indicates that the S level is great enough that N will be efficiently utilized for the formation of plant proteins (Black 1968, Burns 1968).

Concentrations of the 4 measured cations, Ca, Mg, K, and Na, were generally higher in the soil than in any plant component. Exceptions were higher concentrations of Ca in the forest floor and in the bark of *Quercus* trees and K in understory leaves.

Calcium concentrations in the forest floor layer were more than 2.5 times greater than *Quercus* leaves. The content of Ca in bark was nearly 10 times greater than heartwood or sapwood. *Quercus* leaves, live branches, dead branches, standing dead trees, and down-dead trees were all comparable in Ca concentration.

Magnesium concentrations in biomass components were highest in the forest floor layer—approximately 3 times greater than in *Quercus* and understory leaves. In contrast to Ca patterns, Mg concentrations in live branches and standing dead and down-dead trees were significantly lower than in *Quercus* leaves.

Understory leaves were significantly higher in K concentration (1.14%) than were *Quercus* leaves (0.68%) or understory stems (0.64%). Potassium concentrations were about equal for live branches, heartwood, and bark, and about half the concentration found in *Quercus* leaves. Concentration of K in forest floor was substantially lower than in *Quercus* leaves and may reflect the ease with which K is leached from the forest floor relative to the other cations (Attiwill 1968).

Highest concentrations of Na occurred in *Quercus* leaves and in the forest floor. Differences among other biomass components were minor, even though some were statistically significant.

Comparisons of cation levels in *Quercus* leaves with levels in the forest floor were variable between our study and results of the litter bag study of Klemmedson (1992). We showed significantly greater Ca and Mg in the forest floor than in *Quercus* leaves. Klemmedson (1992) found similar increases in Ca in *Quercus* leaves over 750 d. However, Mg concentration in his study declined to about 80% of the level in fresh leaves over the 750-d study. Differences in K concentration that we found between *Quercus* leaves and the forest floor were not nearly as great as the decline in K concentration over time in the litter layer measured by Klemmedson (1992). Potassium concentration in *Quercus* leaves declined about 70% in 500 d and then stabilized to the end of the 750-d study. Differences between Klemmedson's observations and ours were probably a result of the fact that he studied changes in nutrient concentration in the litter layer and our comparisons were with the entire forest floor.

There is little information on the concentrations of nutrients in biomass components in western hardwood stands. There are 2 apparent reasons for this. Compared with the eastern United States, the area occupied by stands of hardwood species in the West is minor. Therefore, until recently, western hardwoods have not been viewed as an economically important resource; rather, they were considered weed species because they were assumed to compete with marketable coniferous trees or with understory forage-producing species. With emerging demands for fuelwood and new markets for unique woods for furniture, there is increased awareness of the value of western hardwoods and, especially, *Q. gambelii* (Wagstaff 1984, Clary and Tiedemann 1992).

Nutrient concentrations of leaves agreed closely with those reported by Klemmedson (1992) for *Q. gambelii* in northern Arizona. Bartos and Johnston (1978) determined the concentrations and proportions of individual nutrients in the various components of 3 clones of *Populus tremuloides* Michx. (quaking aspen) trees in Utah and Wyoming but did not consider the forest floor, understory, and down-dead components of the nutrient pool. Concentrations of N in the various tree components of *Q. gambelii* and *P. tremuloides* were comparable except for higher concentrations of N (2.5%) in leaves of *P. tremuloides*; concentrations of P, K, and Ca were similar for all tree components. Sodium concentrations were generally greater in *Q. gambelii* than in *P. tremuloides*. Concentrations of N, P, and S in live aboveground biomass of *Q. gambelii* were comparable to those reported for *Q. robur* in Russia (Rodin and Bazilevich 1967) and in Belgium (Duvigneaud and Denaeyer-De Smet 1970). Concentrations of N in forest floor and dead branches also were comparable to values for southern and eastern U.S. *Quercus* stands (Lang and Forman 1978). Concentrations of cations in our study did not agree as well with those presented in the literature as for N, P, and S. For example, *Q. gambelii* forest floor concentrations of K and Mg were 3 and 8 times greater than those reported for *Q. robur*. Calcium concentrations in *Q. gambelii* were substantially greater than those observed in other studies in forest floor, live branches, dead branches, standing dead trees, and down-dead trees.

Distribution of Nutrient Capital Among Components

Comparisons of nutrient distribution between above- and belowground components must be considered from the perspective that our soil sampling was restricted to the upper 30 cm because of rock and the massive underground structures of *Q. gambelii*. The actual zone of rooting and nutrient acquisition was undoubtedly much greater than the area we sampled. Therefore, our estimates of the proportions of nutrients in aboveground components were likely to be higher than if the entire rooting zone had been sampled. Also, the kg ha^{-1} estimates were for the area of the actual clone sampled. Clones of *Q. gambelii* do not occupy the entire area of the sites on which they occur. Most studies take into account the high- and low-density areas of tree occupancy in determining nutrient distribution. Therefore, in making projections to an areal basis, the actual area occupied by *Q. gambelii* clones must be considered.

The greatest proportion of total nutrient capital sampled was contained in the soil (Table 2). Of the total capitals of individual nutrients, 82%–99% were contained in the soil. Aboveground accumulations of individual nutrients in live biomass, standing and down-

TABLE 2. Distribution of nutrients among biomass, forest floor, standing plus down-dead, and soil components of *Q. gambelii* stands.

Nutrient	Live[a] aboveground biomass	Standing plus down-dead	Forest[b] floor	Total aboveground	Live[c] belowground biomass	Total[d] live biomass	Soil[e]	Total[f] capital
Nitrogen (kg ha^{-1})	245	140	654	1039	270	515	9500	10810
% of total aboveground	24	13	63					
% of total capital				10	2		88	
Phosphorus (kg ha^{-1})	19	4	48	71	19	38	410	500
% of total aboveground	27	5	68					
% of total capital				14	4		82	
Sulfur (kg ha^{-1})	19	13	46	78	22	41	946	1046
% of total aboveground	24	17	59					
% of total capital				8	2		90	
Calcium (kg ha^{-1})	334	303	1167	1804	924	1258	28844	31571
% of total aboveground	18	17	65					
% of total capital				6	3		91	
Magnesium (kg ha^{-1})	62	35	381	478	63	125	42485	43023
% of total aboveground	13	7	80					
% of total capital				1	<1		99	
Potassium (kg ha^{-1})	201	72	144	417	116	317	20268	20801
% of total aboveground	48	18	34					
% of total capital				2	<1		98	
Sodium (kg ha^{-1})	7	4	20	31	7	14	1765	1804
% of total aboveground	22	13	65					
% of total capital				2	<1		98	
Total (kg ha^{-1})	887	571	2460	3918	1421	2308		
% of total aboveground	23	14	63					
% of total in living biomass	38				62			

[a] Includes living aboveground overstory and understory vegetation.

[b] Includes all forest floor layers above mineral soil.

[c] Includes roots, rhizomes, and lignotubers in the upper 100 cm of soil.

[d] Standing crop plus belowground biomass.

[e] Upper 30 cm of soil.

[f] Standing crop plus standing and down-dead plus forest floor plus belowground biomass plus soil.

dead, and forest floor ranged from 31 kg ha^{-1} for Na to 1804 kg ha^{-1} for Ca. Proportions of total capitals of N, P, and S in aboveground components were highest with 10%, 14%, and 8%, respectively. The proportion of N (the most widely reported nutrient) in aboveground components (10%) was comparable to that described for other semiarid and temperate forest and woodland ecosystems (Klemmedson 1975, Brown 1977, Tiedemann 1987a).

The forest floor was the most important aboveground reservoir of nutrients with 63% of the total accumulation above ground. Accumulations of individual nutrients in the forest floor ranged from 20 to 1167 kg ha^{-1} and constituted 34%–80% of the aboveground capitals.

Total nutrient content of the forest floor in our *Q. gambelii* clones (2460 kg ha^{-1}) substantially exceeded the range described by Lang and Forman (1978) in their summary for U.S. *Quercus* forests (206 kg ha^{-1} [Yount 1975] to 1462 kg ha^{-1} [Gosz et al. 1976]). Greater accumulation of Ca in the forest floor layer (1167 kg ha^{-1}) compared with that reported by other observers (98–400 kg ha^{-1}; Lang and Forman 1978) accounted for much of the difference in total accumulation of nutrient elements in *Q. gambelii* compared with other *Quercus* stands. Also, forest floor biomass accumulation in our *Q. gambelii* stands (37,348 kg ha^{-1}; Clary and Tiedemann 1986) was near the upper limit (46,800 kg ha^{-1}) of that presented for U.S. *Quercus* forests (Lang and Forman 1978).

The massive belowground system of lignotubers, rhizomes, and roots comprised 56% of the total biomass of *Q. gambelii* (Clary and Tiedemann 1986) and contained <1% to 4% of the total of the capitals of individual nutrients. However, relative to the total nutrient accumulation in live biomass, the live belowground component was an important storage area containing 37%–74% of the individual nutrient accumulations. The proportion of total nutrients in belowground biomass (61%) substantially exceeded the range for deciduous forests worldwide (30%–40%) summarized by Rodin and Bazilevich (1967). This finding supported the conclusions of Chattaway (1958), Robbins et al. (1966), and Blake and Carrodus (1970) that storage of nutrients is an important function of belowground components such as lignotubers.

Total content of nutrients in the entire organic component (total live and dead aboveground and belowground biomass) of our *Q. gambelii* stands (5339 kg ha^{-1}) was in the middle of the range for deciduous forests worldwide (2000–7500 kg ha^{-1}) summarized by Rodin and Bazilevich (1967). Similarly, total nutrient content of live biomass (2308 kg ha^{-1}) was comparable to values for oak forests in Russia (2600–3400 kg ha^{-1}; Rodin and Bazilevich 1967).

Worldwide, leaves usually constitute 8%–10% of the store of mineral elements in plant biomass (Rodin and Bazilevich 1967). Mineral element accumulation in *Q. gambelii* leaves and understory leaves (245 kg ha^{-1}; not shown in Table 2) comprised 11% of the total mineral content of live biomass and was within the relatively constant, narrow range of 200–300 kg ha^{-1} normally found in leaves reported by Rodin and Bazilevich (1967).

CONCLUSIONS

Gambel oak appears to be unique from other deciduous forests in the accumulation of nutrients in the forest floor and in belowground biomass components. Both were major areas of nutrient accumulation. The leaves, in contrast, were a minor storage area.

Accumulation of nutrients in aboveground living and dead components expressed as a proportion of total site nutrients was similar to that reported for other semiarid and temperate forest habitats. The quantity of N, the most commonly measured nutrient stored in the forest floor, also agreed well with this literature. It should be noted that had we been able to sample a larger proportion of the total rooting zone, the proportion of the total nutrient capital aboveground would likely have been smaller.

Low levels of P in the upper 30 cm of soil suggest that this element may limit productivity of *Q. gambelii*. Because of potential limitations in the soil, accumulation of 14% (71 kg ha^{-1}) of the total ecosystem P in aboveground living and dead components, we suggest caution in the way the forest floor and residues are managed. Fuelwood harvest followed by removal of residues by broadcast burning could cause large losses of P, depending on degree of consumption of organic matter and fire temperatures (Covington and DeBano 1988, DeBano 1988). This loss may reach 60% (of 71 kg ha^{-1}) if fuels are totally consumed (Raison et al. 1985). However, such losses need to be weighed against changes in P availability that result from burning. In his summary of plant- and litter-contained nutrients, DeBano (1988) indicated that fire-induced increases in P availability decline and reach pre-fire levels within 1 yr. DeBano and Klopatek (1988) showed that inorganic P is released by prescribed burning but is quickly immobilized and may not be readily available for plant growth.

Although there are also substantial accumulations of N and S in aboveground biomass and these are sensitive to losses from volatilization (Knight 1966, Tiedemann 1987b), they are not limiting in the soil and quantities are likely sufficient to replenish losses.

Fertilizer amendment with P may warrant consideration as a means of improving *Q. gambelii* productivity after harvest. This decision, however, should be based on soil tests to determine the availability of P.

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COMPARISON OF TWO ROADSIDE SURVEY PROCEDURES FOR DWARF MISTLETOES ON THE SAWTOOTH NATIONAL FOREST, IDAHO

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ABSTRACT.—Two roadside surveys were conducted for dwarf mistletoes parasitizing lodgepole pine and Douglas-fir on the Sawtooth National Forest, Idaho. One survey used variable-radius plots located less than 150 m from roads. The 2nd survey used variable-radius plots established at 200-m intervals along 1600-m transects run perpendicular to the same roads. Estimates of the incidence (percentage of trees infected and percentage of plots infested) and severity (average dwarf mistletoe rating) for both lodgepole pine and Douglas-fir dwarf mistletoes were not significantly different for the 2 survey methods. These findings are further evidence that roadside-plot surveys and transect-plot surveys conducted away from roads provide similar estimates of the incidence of dwarf mistletoes for large forested areas.

Key words: dwarf mistletoes, surveys, lodgepole pine, Douglas-fir.

Dwarf mistletoes (*Arceuthobium* spp.) are damaging disease agents in many western forests (Hawksworth and Wiens 1995). In the Intermountain West lodgepole pine (*Pinus contorta* Dougl. ex Loud.) and Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco) are the most commonly infected trees (Hawksworth and Wiens 1972, 1995, Hoffman 1979). Each of these hosts is parasitized by a different dwarf mistletoe: lodgepole pine dwarf mistletoe (*A. americanum* Nutt. ex Engelm.) and Douglas-fir dwarf mistletoe (*A. douglasii* Engelm.). Severe infection by these parasites is often associated with tree mortality, reduced growth and cone production, tree deformity, and predisposition to attack by other diseases and/or insects (Hawksworth and Wiens 1995). Therefore, resource managers in many private, state, and federal land-management agencies implement management activities designed to reduce the damage associated with dwarf mistletoes. Because information on the incidence and severity of these pathogens is required by resource managers for making decisions regarding dwarf mistletoe management, surveys are commonly conducted in designated management units (stands) and over larger areas, such as national forests.

Surveys of dwarf mistletoe infection over large areas frequently combine roadside reconnaissance information with data collected using variable-radius or fixed-area plots located near roads (roadside-plot surveys) for estimating the incidence (percent of trees or plots infected) and severity (intensity of infection in individual trees; Hawksworth 1956, 1958, Hawksworth and Lusher 1956, Andrews and Daniels 1960, Graham 1960, 1964, Dooling 1978, Hoffman 1979, Johnson et al. 1980, Johnson et al. 1981, Hoffman and Hobbs 1985, Merrill et al. 1985, Maffei and Beatty 1988). Roadside reconnaissance surveys consist of driving roads at slow speed and recording visual estimates of dwarf mistletoe infection within a short distance from the roadside, usually 20 m. Dwarf mistletoe incidence is estimated by determining the ratio of the number of kilometers surveyed adjacent to infected trees to the total kilometers surveyed adjacent to stands predominated by host trees (Dooling 1978). Roadside-plot surveys involve locating plots near roads at specific intervals and collecting tree data including species, diameter, height, age, and mistletoe severity on each plot. Dwarf mistletoe incidence has typically been represented by the percentage of plots infested with mistletoe, rather than the percentage of trees infected in all plots (Dooling 1978).

Roadside surveys have the benefit of allowing large areas to be surveyed rapidly and inexpensively. In addition, roadside surveys concentrate efforts in areas that are accessible and more likely to be considered for management actions. Concerns about the reliability of roadside survey methods are primarily related to the bias that may be encountered by sampling mistletoe incidence and severity near roads because roads are typically constructed according to topographic features (in drainages or along ridgetops) rather than randomly or systematically located throughout the survey area. Since there is evidence that dwarf mistletoe distribution is related to topography (Hawksworth 1959, 1968), these concerns need to be considered when conducting dwarf mistletoe surveys over large forested areas.

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Because few surveys have compared data collected from roadside reconnaissance or roadside-plot surveys with data collected from more intensive, random or systematic surveys for dwarf mistletoes over large areas (Hawksworth 1956, 1958, Johnson et al. 1981, Merrill et al. 1985), we initiated this study to compare dwarf mistletoe incidence and severity estimates obtained from roadside-plot surveys with those from transect-plot surveys that sampled areas at greater distances from roads. We surveyed 3 districts of the Sawtooth National Forest, Idaho, because this national forest is representative of forests in the Intermountain West where lodgepole pine and Douglas-fir are the predominant tree species and dwarf mistletoes are common (Hoffman 1979, Hoffman and Hobbs 1985).

METHODS

We used a roadside-plot survey and a transect-plot survey to collect dwarf mistletoe incidence and severity data in 3 adjacent districts (Ketchum Ranger District, Fairfield Ranger District, and Sawtooth National Recreation Area) of the Sawtooth National Forest, Idaho, in 1990. We surveyed each district by arbitrarily selecting a major road system in each township containing ≥ 10 sections of federally managed land. Townships with no roads or with few roads were not sampled. Road systems were chosen before fieldwork began, and adjustments were made in the field only when selected road systems were closed or impassable.

Roadside-plot Survey

Field crews arbitrarily chose a starting reference point on each selected road system. Starting reference points were landmarks that could easily be relocated such as a bridge, stream crossing, or road junction. Crews drove a distance of 800 m from the starting reference point toward the center of each township. They then selected a compass bearing perpendicular to the right-hand side of the road and located an end point 120 m from the road. Three 20 basal area factor variable-radius plots (point samples; Avery and Burkhart 1983) were established 40 m from this end point at compass bearings of 240°, 120°, and 0° from the compass bearing used to locate the end point. Crews then drove another 800 m down the road and established a 2nd cluster of 3 variable-radius plots using the same procedure. For each plot tree the following information was recorded: plot number, species, diameter at 1.37 m aboveground (nearest 0.25 cm), status (live or dead), and dwarf mistletoe rating (DMR, 6-class system; Hawksworth 1977). If a plot did not contain trees, it was recorded as nonstocked.

Transect-plot Survey

A 1600-m (approximately 1-mi) transect perpendicular to the road was run along the same compass bearing used for establishing the 1st set of roadside plots (800 m from the starting reference point) in each township surveyed. A 20 basal area factor variable-radius plot was located every 200 m along each transect for a total of 8 plots. Information recorded for plot trees was the same as above.

Analyses

The incidence of each species of dwarf mistletoe (percentage of trees infected) was calculated for each set of roadside plots (up to 6 plots) and each set of transect plots (up to 8 plots) for each township. Incidence was calculated on a per-hectare basis by multiplying by per-hectare conversion factors based on 2.54-cm-diameter classes for 20 basal area factor variable-radius plots (Avery and Burkhart 1983). Weighted dwarf mistletoe ratings were calculated by multiplying the DMR of each tree by the per-hectare conversion factors also. These weighted values were used to calculate the mean percentage of trees infected and mean dwarf mistletoe rating for each survey procedure in each township on a per-hectare basis. These values were then used to calculate the percentage of trees infected and a mean DMR for each tree species and survey method.

Data from townships where the surveys did not sample at least 3 Douglas-fir or lodgepole pine for each of the survey procedures were not included in the analyses. Only living trees were used in the analyses for calculating mean DMR because it was not always possible to accurately assign a DMR to dead trees. Incidence values were calculated for 9 townships for lodgepole pine and for 17 townships for Douglas-fir. The roadside-plot survey sampled a total of 206 lodgepole pine and 357 Douglas-fir in 46 and 75 plots, respectively. The transect-plot survey sampled 171 lodgepole pine and 342 Douglas-fir in 42 and 87 plots, respectively. A one-way analysis of variance (ANOVA, $P > 0.05$) was used to determine if the mean values for incidence and severity were significantly different between the 2 survey procedures. Percentages were converted using arcsin transformations before ANOVA analyses were performed (Snedecor and Cochran 1989).

To compare our results with those of other dwarf mistletoe surveys, we determined incidence of both dwarf mistletoes for both survey procedures by calculating the percentage of plots infested. If a plot had at least 1 infected tree, it was considered infested. This method of reporting dwarf mistletoe incidence has been applied in the majority of roadside-plot surveys conducted for dwarf mistletoes in the western United States.

RESULTS AND DISCUSSION

Mean diameters for trees sampled using each survey method were approximately the same for lodgepole pine and Douglas-fir (Table 1). Sampled tree diameters were clearly skewed toward larger trees (Table 1) because both survey methods used variable-radius plots that sample large trees more often than small trees (Avery and Burkhart 1983). Because both survey methods sampled trees in the same way, the survey results should be comparable. However, it is probable that the percentage of infected trees and mean DMR would have been lower for both lodgepole pine and Douglas-fir had more small trees been sampled because small trees are typically less often and less severely infected (Parmeter 1978).

Estimates of incidence for Douglas-fir dwarf mistletoe using the 2 survey methods were within 3% of each other based on the percentage of trees infected (Table 2). Estimates of Douglas-fir dwarf mistletoe severity were similar also. The differences between Douglas-fir dwarf mistletoe incidence and severity for the 2 survey methods were not statistically significant. The differences between estimates of the incidence and severity of lodgepole pine dwarf mistletoe for the 2 survey methods were larger than for Douglas-fir dwarf mistletoe (Table 3). However, the differences were not significant. Therefore, the 2 survey methods

TABLE 1. Distribution of lodgepole pine and Douglas-fir sampled by diameter classes for the roadside-plot and transect-plot surveys on the Sawtooth National Forest, Idaho.

	Lodgepole pine				Douglas-fir			
	Roadside-plot		Transect-plot		Roadside-plot		Transect-plot	
Diameter class (cm)	Mean diameter (cm)	*N*	Mean diameter (cm)	*N*	Mean diameter (cm)	*N*	Mean diameter (cm)	*N*
2–13	9.1	47	8.6	39	10.6	17	9.1	10
14–25	19.6	108	19.8	92	20.6	90	20.1	108
26–38	29.2	39	30.0	34	31.8	98	32.0	99
39–51	41.9	7	42.9	5	43.7	85	44.7	60
52–64	60.7	5	51.1	1	56.6	32	57.4	24
>64	—[a]	—	—	—	96.5	35	89.4	41
TOTAL	20.8	206	20.1	171	39.5	357	40.9	342

[a] No trees sampled in this size class.

TABLE 2. Incidence and severity of Douglas-fir dwarf mistletoe estimated from roadside-plot and transect-plot surveys on the Sawtooth National Forest, Idaho.

	Incidence		Severity	
Survey method	Mean percent infected[a]	95% mean confidence limit	Mean DMR[b]	95% mean confidence limit
Roadside-plot	28.4[c]	11.0–45.8	0.9[c]	0.2–1.5
Transect-plot	25.8	10.0–41.5	0.8	0.2–1.4

[a] Based on the percentage of individual trees infected on a per-hectare basis

[b] Dwarf mistletoe rating (Hawksworth 1977)

[c] Means in this column are not significantly different; one-way ANOVA, $P > 0.05$.

TABLE 3. Incidence and severity of lodgepole pine dwarf mistletoe estimated from roadside-plot and transect-plot surveys on the Sawtooth National Forest, Idaho.

	Incidence		Severity	
Survey method	Mean percent infected[a]	95% mean confidence limit	Mean DMR[b]	95% mean confidence limit
Roadside-plot	48.5[c]	29.4–67.5	1.2[c]	0.6–1.8
Transect-plot	55.7	35.3–76.1	1.6	1.1–2.1

[a] Based on the percentage of individual trees infected on a per-hectare basis

[b] Dwarf mistletoe rating (Hawksworth 1977)

[c] Means in this column are not significantly different; one-way ANOVA, $P > 0.05$.

provided equivalent estimates of dwarf mistletoe incidence, based on the percentage of trees infected, and severity for both dwarf mistletoes.

Dwarf mistletoe incidence based on the percentage of plots infested is presented in Table 4. Both survey methods provided estimates that were within 2% of each other for both dwarf mistletoes. Calculating dwarf mistletoe incidence based on the percentage of plots infested greatly increases the estimates of dwarf mistletoe incidence when compared to the incidence based on the percentage of trees infected because it requires only 1 infected tree for a plot to be treated as infested.

Lodgepole pine dwarf mistletoe is one of the most widely distributed dwarf mistletoes in the western United States (Hawksworth and Wiens 1995). The incidence of this mistletoe, based on the percentage of plots infested, has varied between approximately 40% and 70% for the majority of national forests surveyed, and averages about 50% (Hawksworth 1958, Graham 1960, 1964, Johnson et al. 1980, 1981, Hoffman and Hobbs 1985). The incidence of lodgepole pine dwarf mistletoe, based on the percentage of plots infested estimated from our surveys in the Sawtooth National Forest (approximately 80%), is higher than for most national forests surveyed thus far. An earlier dwarf mistletoe survey of the Sawtooth National Forest (Hoffman and Hobbs 1985) reported the incidence of lodgepole pine dwarf mistletoe as 71%. However, that survey did not include the Sawtooth National Recreation Area, the district in which we detected a very high incidence of lodgepole pine dwarf mistletoe (83%). Therefore, the Sawtooth National Forest probably does have a higher incidence of lodgepole pine dwarf mistletoe than many other western national forests.

An earlier estimate of the incidence of Douglas-fir dwarf mistletoe, based on the percentage of plots infested, for the Sawtooth National Forest was 53% (Hoffman 1979). Although that survey sampled only the southern districts of the Sawtooth National Forest and did not include the districts we surveyed, our estimate for Douglas-fir dwarf mistletoe, based on the percentage of plots infested, is approximately the same (almost 50%).

Our findings provide additional evidence that estimates of incidence and severity of dwarf mistletoes using roadside-plot surveys

TABLE 4. Incidence of Douglas-fir and lodgepole pine dwarf mistletoes based on the percentage of plots infested estimated from roadside-plot and transect-plot surveys on the Sawtooth National Forest, Idaho.

	Douglas-fir dwarf mistletoe		Lodgepole pine dwarf mistletoe	
Survey method	Plots	Percent infested	Plots	Percent infested
Roadside-plot	75	47	46	80
Transect-plot	87	48	42	78

approximate those of similar surveys conducted away from roads. Hawksworth (1956) reported similar results based on a more intensive comparison of roadside-plot and transect-plot surveys for dwarf mistletoes on the Mescalero Apache Indian Reservation, New Mexico. Partridge and Canfield (1980) compared the incidence of several forest pests in southern Idaho estimated using roadside-plot surveys and plots randomly located in areas without roads. They reported no discernible differences between the incidence of the pests detected (including dwarf mistletoes) for the 2 survey procedures. Because this study and others indicate that roadside-plot surveys provide similar estimates of dwarf mistletoe incidence to surveys conducted away from roads, we recommend that resource managers continue to use roadside-plot surveys for estimating dwarf mistletoe incidence for national forests or other large forested areas. However, because these surveys sample only a small fraction of the survey area, they will provide only rough estimates of the incidence and severity of dwarf mistletoes.

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EFFECTS OF DOUGLAS-FIR FOLIAGE AGE CLASS ON WESTERN SPRUCE BUDWORM OVIPOSITION CHOICE AND LARVAL PERFORMANCE

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ABSTRACT.—The western spruce budworm (*Choristoneura occidentalis* Freeman) prefers to feed on flushing buds and current-year needles of Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco). Budworm larvae will not typically consume older age classes of needles unless all current-year foliage is depleted. We tested the following null hypotheses: (1) budworm larvae can feed on foliage with a wide range of qualities (i.e., current-year versus 1-, 2-, or 3-year-old needles) without measurable effects on fitness; and (2) budworm adults do not show any oviposition preference linked to the age of the foliage they fed on as larvae. We used both laboratory and field experiments. There was strong evidence to support rejection of hypothesis 1. Budworm larvae had greater survival from the 4th instar to pupal stage when they fed on current-year foliage (43%–52% survival) versus older age classes of foliage (0–25% survival). Pupae from current-year foliage were also heavier than pupae from ≥1-year-old foliage. There was weak evidence to support rejecting hypothesis 2; budworm adults that had fed on current-year or 3-year-old foliage as larvae preferred to oviposit on current-year foliage. Similar conclusions were drawn from the laboratory and field experiments.

Key words: Choristoneura occidentalis, *western spruce budworm, oviposition preference, needle age, foliar quality, eruptive species.*

The western spruce budworm (*Choristoneura occidentalis* Freeman) is a major defoliator of Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco) trees in western North America (Fellin and Dewey 1982, Wulf and Cates 1987, Clancy et al. 1988). Budworm larvae prefer to feed on the flushing buds and current-year needles of their host trees. However, if all current-year foliage is depleted, larvae will feed on older needles (Fellin and Dewey 1982, Talerico 1983, Blake and Wagner 1986). Previous experiments by Talerico (1983) and Blake and Wagner (1986) show older foliage is suboptimal, resulting in reduced fecundity, higher mortality rates, and impaired development. When budworm larvae are forced to feed on only mature foliage, they have reduced growth, lower pupal weights, and decreased survival, or they may not survive at all (Blake and Wagner 1986).

Variations in host foliage quality may influence the feeding and oviposition behavior of the western spruce budworm (Clancy et al. 1988). Differences in levels of foliar nutrients, water content, needle toughness, etc., between current-year and older (≥1-year-old) age classes of needles impact the budworm's fecundity, growth rate, and survivorship (Mattson and Scriber 1987, Clancy et al. 1988, Clancy 1991b, 1991c), and may influence female oviposition choices.

However, the budworm's oligophagous feeding behavior and eruptive population dynamics suggest it is unlikely that there is a tight linkage between female oviposition preference and larval performance (Price et al. 1990). Female moths do not determine where their offspring will feed. Budworm adults lay eggs on mature foliage in late summer (Furniss and Carolin 1977, Brookes et al. 1987); upon hatching, the 1st instars (which do not feed) disperse to sheltered locations (e.g., beneath bark scales), where they spin a hibernaculum and overwinter. When larvae emerge from their hibernacula the following spring, they disperse again (typically on silken threads) to find appropriate food sources. The budworm's life history suggests that neither adults nor larvae actively select host foliage based on differences in nutritional quality among individual host trees. Instead, larvae passively disperse from their overwintering sites and may land on acceptable food sources. Once larvae are on a host tree, they search for expanding current-year buds and needles. If suitable foliage is not available, larvae can disperse horizontally or vertically within and between tree crowns and stands, but dispersal invariably results in significant losses; whether dispersing larvae live or die depends largely on whether they find hospitable sites (Brookes et al. 1987). Therefore, the ability to utilize a broad range of foliage qualities would be advantageous for budworm survival.

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This study was designed to compare results from laboratory and field tests of the null hypotheses that (1) budworm larvae can feed on foliage with a wide range of qualities (i.e., current-year versus 1-, 2-, or 3-year-old needles) without measurable effects on fitness; and (2) budworm adults do not show any oviposition preference linked to the age of the foliage they fed on as larvae. Furthermore, we wanted to determine if conclusions drawn from laboratory versus field experiments were similar. This is important because many previous studies conducted with budworms and other forest defoliators have used clipped foliage without knowing the effects this may have on foliar nutrition or host defenses. By conducting parallel experiments using intact and excised foliage from the same trees, we were able to evaluate the importance of changes in foliar quality that may be associated with bagging larvae on intact branches in the field versus feeding larvae excised foliage in the laboratory.

STUDY AREA AND ORGANISMS

The study area is located at Little Springs (elevation 2560 m), 16 km north of Flagstaff, Arizona, within the Coconino National Forest. The site is a high-elevation, mixed-conifer forest, with Douglas-fir as the primary host species and with a recent history of western spruce budworm infestation.

The western spruce budworm has a univoltine life cycle. Adults are present from July to August, with mating typically occurring within 24 h of eclosion. Eggs are laid soon after mating; females lay between 25 and 40 eggs per egg mass (Brookes et al. 1987). Eggs hatch in about 10 d; after dispersing to sheltered locations and spinning a hibernaculum, larvae molt into 2nd instars and overwinter. In spring, the 2nd instars emerge from diapause, feed through the 6th instar, and pupate in late June or early July. Adults eclose within 10 d. Our laboratory population of nondiapausing western spruce budworm differs in that there is no overwintering stage.

METHODS

Field Experiment

To determine larval performance in the field, we selected and tagged 50 Douglas-fir trees of various sizes and ages on 1–2 June 1993. All tagged trees had abundant foliage in the lower crown. Sleeve bags made of fine mesh screen were placed over 4 branches on each of the 50 trees, and each bagged branch was randomly assigned to a foliage age class (current-year, 1-year-, 2-year-, or 3-year-old needles). We removed by hand all needles that were not of the appropriate age class. Any wild budworms present on the bagged branches were also removed.

On 4 and 8 June, two 4th or early 5th instar budworm larvae from our laboratory culture were placed on foliage inside each bagged branch (a total of 400 larvae were used); this constituted the parental (P_1) generation. We have established that budworm larvae from our laboratory culture have rates of survival and reproduction equivalent to wild budworms when reared on Douglas-fir foliage in the field (Leyva et al. 1995). Bags were closed with string or duct tape at each end. We examined the bagged branches on 20 June to determine if sufficient foliage remained for completion of larval development. Pupae were not observed at this time.

Budworm larvae remained in the field until about half of them had pupated, and then the bagged branches were clipped, placed inside large plastic bags, and transported to the laboratory. Pupae were weighed (to the nearest 0.1 mg), sorted into trays according to treatment (foliage age class) and sex, and then refrigerated at 10°C until we obtained 10 males and 10 females from the same treatment. Larvae that had not pupated were placed in labeled petri dishes lined with moist filter paper. Douglas-fir foliage of the appropriate age class was provided for them to feed on until they pupated; this foliage was collected at random from tagged Douglas-fir trees at the study site. Foliage was replaced every 2–3 d to ensure freshness. Petri dishes were checked each Monday, Wednesday, and Friday to remove and weigh new pupae (these were also sorted and refrigerated).

When 10 pairs of male and female pupae were available from a treatment, they were placed in a brown paper mating bag; oviposition preference tests for both field and laboratory experiments were conducted in the laboratory. Brown paper bags provided appropriate lighting conditions both for mating (which occurs from 2000 to 2300 h in nature), when only safety lights were on in the laboratory at night, and for oviposition (which normally occurs the day following mating), when all lights were on during the day (i.e., bags are not opaque). Bags were checked every other day until 5 or 6 moths emerged; then branches of freshly clipped Douglas-fir foliage were added for oviposition substrate. Once foliage was added, moths were allowed to mate and oviposit for 7–8 d. After oviposition occurred, Douglas-fir branches were removed and inspected for egg masses. These F_1 egg masses were sorted according to treatment (foliage age class) to determine if female moths showed a preference for ovipositing on a particular age class of foliage.

The F_1 egg masses collected were surface-sterilized with formalin and placed into labeled cups containing an artificial diet nutritionally similar to Douglas-fir foliage (Clancy 1991a). F_1 larvae were reared on the diet until the 4th or early 5th instar stage, after which they were placed in labeled petri dishes lined with moist filter paper. Douglas-fir foliage of the same age class that their parents consumed was provided for them to feed on until they pupated; this foliage was collected at random from tagged Douglas-fir trees at the study site. These larvae were not placed in the field because it was too late in the season for conditions suitable for budworm development. Foliage was replaced every other day to ensure freshness. F_1 larvae were reared on foliage within petri dishes until they pupated; pupae were handled in the same manner as in the first generation.

Laboratory Experiment

This study was conducted to determine if laboratory experiments using excised foliage would yield results similar to those from field experiments using intact foliage. The experiment was started 24 June 1993. Douglas-fir foliage used in this experiment was collected from the same 50 trees we used for the field experiment. Four hundred 4th instar budworms were placed on excised foliage in petri dishes lined with moist filter paper, 2 larvae per dish. Fifty petri dishes were used per foliage age class treatment (current-year, 1-year-, 2-year-, and 3-year-old needles), corresponding to the 50 trees used in the field experiment. Needles of the appropriate age class were left attached to the stem to prevent desiccation of foliage. Foliage was replaced every 2–3 d to ensure freshness. Petri dishes were labeled according to the tree number and foliage age class. If a single larva or both larvae in each petri dish died before pupation, they were replaced with new larvae from our laboratory culture. Otherwise, we used the same procedures for the laboratory experiment as for the field experiment.

RESULTS

Effects of Foliage Age Class on P_1 Survival and Pupal Weight

Budworm larvae that consumed current-year needles of Douglas-fir in the field experiment had higher survival rates from 4th instar to pupal stage (43% survival) compared to larvae that fed on 1-year-old (2% survival), 2-year-old (1% survival), or 3-year-old (0% survival) needles (Fig. 1A) ($\chi^2 = 130.19$, df = 3, $P < 0.001$, $n = 400$). We believe that many of the larvae bagged on the branches with only ≥1-year-old needles to feed on escaped from the mesh bag enclosures, so it may be more appropriate to refer to this response as "percent larvae accounted for" rather than "percent larval survival." Larvae from older foliage age class treatments were more likely to escape because budworm larvae tend to disperse when suitable food is not available, and our bags were not so tightly sealed that larvae could not wriggle out through small openings along the seams or closures at the ends.

The age class of foliage ingested had a similar effect on survival from 4th instar to pupal stage in the laboratory experiment (Fig. 1B) ($\chi^2 = 59.46$, df = 3, $P < 0.001$, $n = 727$). Approximately 52% of larvae that consumed current-year needles survived. Survival was 25% for larvae consuming 1-year-old needles, 18% for larvae feeding on 2-year-old needles, and 20% for larvae eating 3-year-old needles.

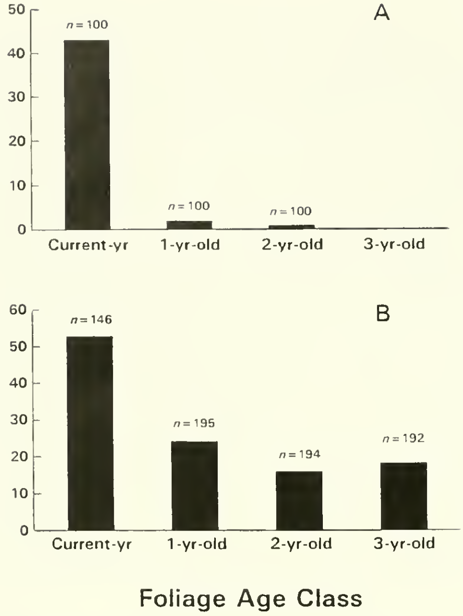

Fig. 1. Percentage of P_1 4th instar western spruce budworms surviving to the pupal stage when reared on current-, 1-, 2-, and 3-year-old Douglas-fir needles for the (A) field experiment and (B) laboratory experiment. χ^2 tests showed that survival varied among the foliage age classes for both the field ($P < 0.001$) and laboratory ($P < 0.001$) experiments. Numbers above the bars indicate sample sizes, i.e., number of budworm larvae used per treatment.

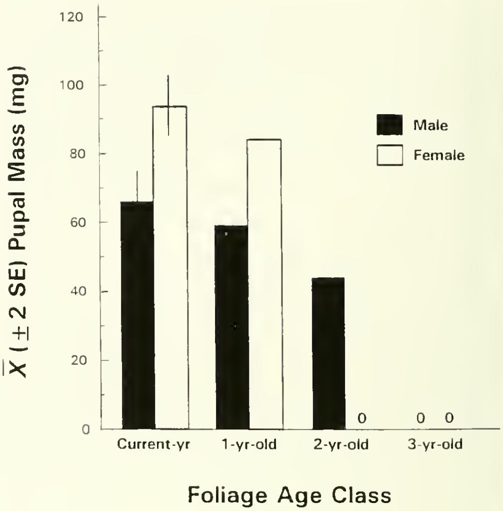

Fig. 2. Mean (±2 s, or ≈95% confidence interval) P_1 male (■) and female (□) pupal weight for larvae reared from the 4th instar to pupation on foliage of different age classes in the field experiment. ANOVA tests showed that foliage age class did not affect pupal weight ($P = 0.152$) and that females weigh more than males ($P < 0.001$). Bars without standard errors had a sample size of $n = 1$.

Foliage age class did not have a significant effect on pupal masses for the field experiment ($F = 1.97$, df = 2,41, $P = 0.152$; Fig. 2). This inability to detect differences among foliage age classes can be attributed to the very small sample sizes ($n = 0$–2) for ≥1-year-old foliage. As expected, female pupae were heavier than male pupae ($F = 20.39$, df = 1,41, $P < 0.001$).

There were detectable differences in pupal masses among different foliage age classes for the laboratory experiment ($F = 36.47$, df = 3,182, $P < 0.001$; Fig. 3). Larvae consuming current-year foliage became much heavier pupae than larvae feeding on ≥1-year-old foliage. Once again, female pupae were bigger than male pupae ($F = 14.70$, df = 1,182, $P < 0.001$).

Effects of Foliage Age Class on Oviposition Preference of P_1 Females

Sample sizes for the field experiment were not large enough for data analysis ($n = 2$ egg masses), but a contingency table analysis of data from the laboratory experiment indicated a dependence between age class of foliage on which the P_1 female was reared and age class of foliage on which the moths laid their F_1 egg masses ($P = 0.017$; Table 1). This was not a very strong test of the hypothesis because there were many zero values in the table, which required that 1-year-, 2-year-, and 3-year-old age class columns and rows be combined to meet requirements for minimum expected cell frequencies. Furthermore, many F_1 egg masses were very small (areas ≤ 3 mm^2); such small egg masses are nearly always inviable and are probably aberrant (Leyva et al. 1995). Nonetheless, the distribution of F_1 egg masses indicated that moths reared as larvae on current-year or 3-year-old foliage laid more of their F_1 egg masses on current-year needles than on older age classes of needles.

Effects of Foliage Age Class on F_1 Survival and Pupal Weight

Only 2 F_1 egg masses were produced from the field experiment. This precluded analyzing data on survival or pupal weights for this experiment. For the laboratory experiment, we found a significant difference in survival from 4th instar to pupal stage between larvae reared on current-year (83.3% survival) versus 3-year-old (30.8% survival) needles ($\chi^2 = 11.78$, df =

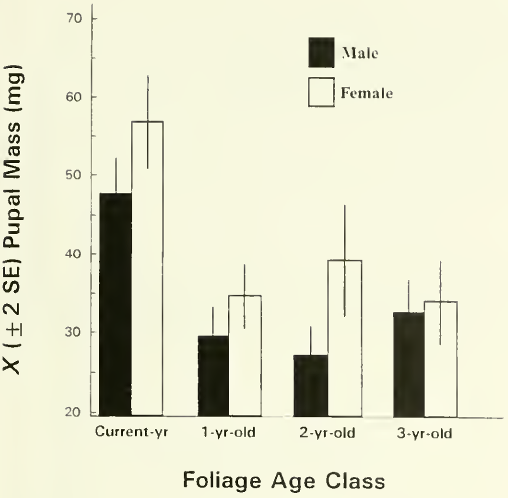

Fig. 3. Mean (± 2 *s*, or ≈95% confidence interval) P_1 male (■) and female (□) pupal weight for larvae reared from the 4th instar to pupation on foliage of different age classes in the laboratory experiment. ANOVA tests showed that foliage age class had a significant effect on pupal weight ($P < 0.001$), as did sex ($P < 0.001$).

1, $P = 0.0006$, $n = 44$). Sample sizes were 0 for 1-year- and 2-year-old needles. This result was consistent with results for the P_1 generation in that survival was higher for larvae reared on current-year foliage than on 3-year-old needles.

However, F_1 pupal masses were equivalent for pupae from current-year and 3-year-old foliage ($F = 1.14$, df = 1,19, $P = 0.299$). As before, female pupae were larger than male pupae ($F = 6.01$, df = 1,19, $P = 0.024$).

DISCUSSION

Although the western spruce budworm's life history and population dynamics suggest that larvae should be able to utilize a broad range of foliage qualities, our results confirm previous studies that indicate the budworm is not well adapted to feeding on 1-year-old or older needles (Talerico 1983, Blake and Wagner 1986). Thus, we must reject hypothesis 1 and conclude that the budworm cannot feed on foliage with as wide a range in qualities as is found in current-year versus ≥1-year-old needles without measurable effects on fitness. We found that whether budworm larvae were feeding on bagged foliage in the field or on excised foliage in the laboratory, larval survival (Fig. 1) and pupal masses (Figs. 2, 3) declined for larvae feeding on ≥1-year-old needles compared to larvae feeding on current-year foliage. The same patterns in relation to the effects of foliage age on survival were evident for both the P_1 and F_1 generations of the laboratory experiment. It is well established that the nutritional quality of Douglas-fir needles declines rapidly as current-year needles age (Clancy et al. 1988, 1995). Furthermore, Clancy et al. (1995) point out that

> the general pattern for 1-year or older needles of conifers is typically an extension of the seasonal trends for nutrient concentration changes in current-year needles.

Needle toughness and fiber content also increase as foliage matures, thus making older needles less suitable food for the budworm. On the other hand, the fact that budworm larvae could survive at all when reared on older age classes of needles may indicate that their nutritional niche is indeed broad, as suggested by Price et al. (1990) and Leyva et al. (1995).

We found less-convincing evidence to support rejection of hypothesis 2, but nonetheless we conclude that budworm adults may show an oviposition preference that is linked to the age of the foliage they fed on as larvae (Table 1). Budworm females that fed as larvae on current-year foliage laid more egg masses on current-year needles than on older needles; females reared on 3-year-old foliage also laid more egg masses on current-year needles. This result is surprising because the budworm typically oviposits on mature foliage (Brookes et al. 1987, Price et al. 1990). However, many egg masses from our experiment were very small and are most likely aberrant (Leyva et al. 1995); thus, we suspect this may not represent normal oviposition behavior for the budworm. If we remove these very small egg masses from the data set, most egg masses were laid on 3-year-old needles, indicating the budworm does indeed prefer to oviposit on mature foliage. An alternative explanation may be that female moths distribute egg masses randomly across age classes of needles available. Current-year needles represent a small proportion of total needles present under natural conditions, and they may be nearly absent when defoliation is heavy. Thus, our result could be an artifact of providing an atypical distribution of needle age classes for oviposition substrate.

TABLE 1. Distribution of F_1 egg masses of the western spruce budworm laid on current-, 1-, 2-, or 3-year-old needles of Douglas-fir, in relation to the age class of the foliage on which the P_1 moths were reared[a].

Age class of foliage on which F_1 egg masses were laid	Age class of foliage on which P_1 female was reared[b]			
	Current-year	1-year-old	2-year-old	3-year-old
Current-year	27	0	0	14
1-year-old	6	0	0	0
2-year-old	5	0	0	1
3-year-old	11	0	0	0

[a] Data are the number of F_1 egg masses from the laboratory experiment. The distribution of egg masses was examined for row-column dependence using a 2 × 2 contingency table (current-year versus ≥ 1-year-old foliage; older foliage age classes were combined in order to meet requirements for minimum expected cell frequencies); Yates-corrected $\chi^2 = 5.725$, df = 1, $P = 0.017$, $n = 64$.

[b] P_1 budworm larvae were reared on foliage of different age classes from the 4th instar to pupation.

Conclusions from the field versus laboratory experiments were similar in regard to the effects of foliage age class on larval survival and pupal masses. This indicates that foliar quality does not change dramatically when foliage is excised (at least not over a 2–3 d period), nor does intact foliage on bagged branches change markedly in terms of a local or systemic-induced response to budworm defoliation.

It is noteworthy that pupae from the current-year foliage treatment in the field experiment were heavier than equivalent pupae from the laboratory experiment (Figs. 2, 3). This difference may well be related to the 15–19 d delay between the start of the field experiment (initiated on 4 and 8 June 1993) and the beginning of the laboratory study (initiated on 24 June 1993), with the concomitant decline in nutritional quality of the expanding current-year foliage. Alternatively, current-year needles remaining on bagged branches could have acted as a local nutrient sink in the absence of competing older needles, which were removed. Thus, larvae feeding on bagged branches with current-year foliage may have benefited from this improved nutritional quality, whereas larvae that were fed clipped foliage in the laboratory experiment would not have received this nutritional boost.

Survival rates were higher overall in the laboratory experiment than in the field experiment (Fig. 1). We attribute this difference to a combination of factors. For example, larvae on bagged branches in the field were exposed to some predation since the bags were not perfect barriers. Also, some budworm larvae undoubtedly escaped from the bags, and weather could have played a role in the lower survival of larvae in the field.

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TRYPANOPLASMA ATRARIA SP. N. (KINETOPLASTIDA: BODONIDAE) IN FISHES FROM THE SEVIER RIVER DRAINAGE, UTAH

J. Stephen Cranney[1] and Richard A. Heckmann[2]

ABSTRACT.—A total of 181 fishes belonging to 10 species were captured near Richfield, Utah, and examined for parasites. A new species of hemoflagellate, *Trypanoplasma atraria* sp. n., was observed in 3 species: Utah chub (*Gila atraria* [Girard]), redside shiner (*Richardsonius balteatus* [Richardson]), and speckled dace (*Rhinichthys osculus* [Girard]). Seven other species of fishes examined in the study area were negative for *T. atraria* sp. n. The salmonid leech, *Piscicola salmositica* (Meyer), collected in the same area harbored developmental stages of *Trypanoplasma*, suggesting a possible leech vector for the hemoflagellate. Characteristics of *Trypanoplasma atraria* sp. n. place it near *T. salmositica*, but the new species is twice as large.

Key words: Trypanoplasma atraria *n. sp., blood parasites,* Gila atraria, *fish parasites.*

Trypanoplasma is a biflagellated protozoan found in the blood of freshwater fishes in the United States. It has caused significant mortality in rainbow trout (*Oncorhynchus mykiss* [Walbaum]) and king salmon (*O. tshawytscha* [Walbaum]) under hatchery conditions (Becker and Katz 1966, Wales and Wolf 1995). This genus has also been described from the blood of marine fish (Strout 1965). Another name for the blood biflagellate of salmonids described above is *Cryptobia*. There are differing opinions on the use of the two genera, *Cryptobia* and *Trypanoplasma*, but these differences have been recently clarified by Lom and Dykova (1992).

The genus *Cryptobia* was first proposed by Leidy (1846) for biflagellated protozoans occurring as parasites in the seminal vesicles of snails. Chalachnikow (1888) was the first to record the parasite in the blood of fishes, observing it in freshwater loaches in Russia. Laveran and Mesnil (1901) established the genus *Trypanoplasma* for a biflagellated blood parasite from freshwater fishes in France. In 1909, Crawley stated that *Cryptobia* from snails and *Trypanoplasma* from fishes were morphologically identical, and that *Cryptobia* had taxonomic priority. In defending the creation of the genus *Trypanoplasma*, Laveran and Mesnil (1912) argued that morphological similarities were not sufficient criteria for maintaining a single genus when strong biological differences, such as method of infection, were evident. The parasites in snails were transferred directly during copulation, while a leech vector was necessary to transfer the flagellate from the blood of one fish to another. Putz (1970) submitted that comparative biological studies between similar morphological types are necessary for a correct taxonomic classification. Use of the genus *Cryptobia* has, in most cases, emerged as the popular choice, and *Trypanoplasma* is generally recognized as a synonym. Recently, Lom and Dykova (1992) used *Trypanoplasma* for biflagellated blood-inhibiting parasites of fishes in which a leech vector is involved. Thus, we adopted the classification scheme used by Lom and Dykova (1992).

Four species of *Trypanoplasma* from the blood of freshwater fishes have been reported in North America. Mavor (1915) found *T. borreli* in a moribund white sucker (*Catostomus commersoni* [Lacepe]) from Lake Huron. The identification of *T. borreli* was based on similarities with the species initially described by Laveran and Mesnil (1901). Katz (1951) recorded *C. (=Trypanoplasma) salmositica* from silver salmon (*O. kisutch* [Walbaum]) and *C. (=Trypanoplasma) lynchi* from cottids in the state of Washington. Subsequent transmission studies showed *C. lynchi* to be a synonym of *C. salmositica* (Becker and Katz 1965a). Laird (1961) described *C. (=Trypanoplasma) gurneyorum* from northern pike (*Esox lucius* [Linnaeus]) and from 2 salmonids: lake whitefish (*Coregonus clupeaformis* [Mitchill]) and lake trout (*Salvelinus namaycush* [Walbaum]).

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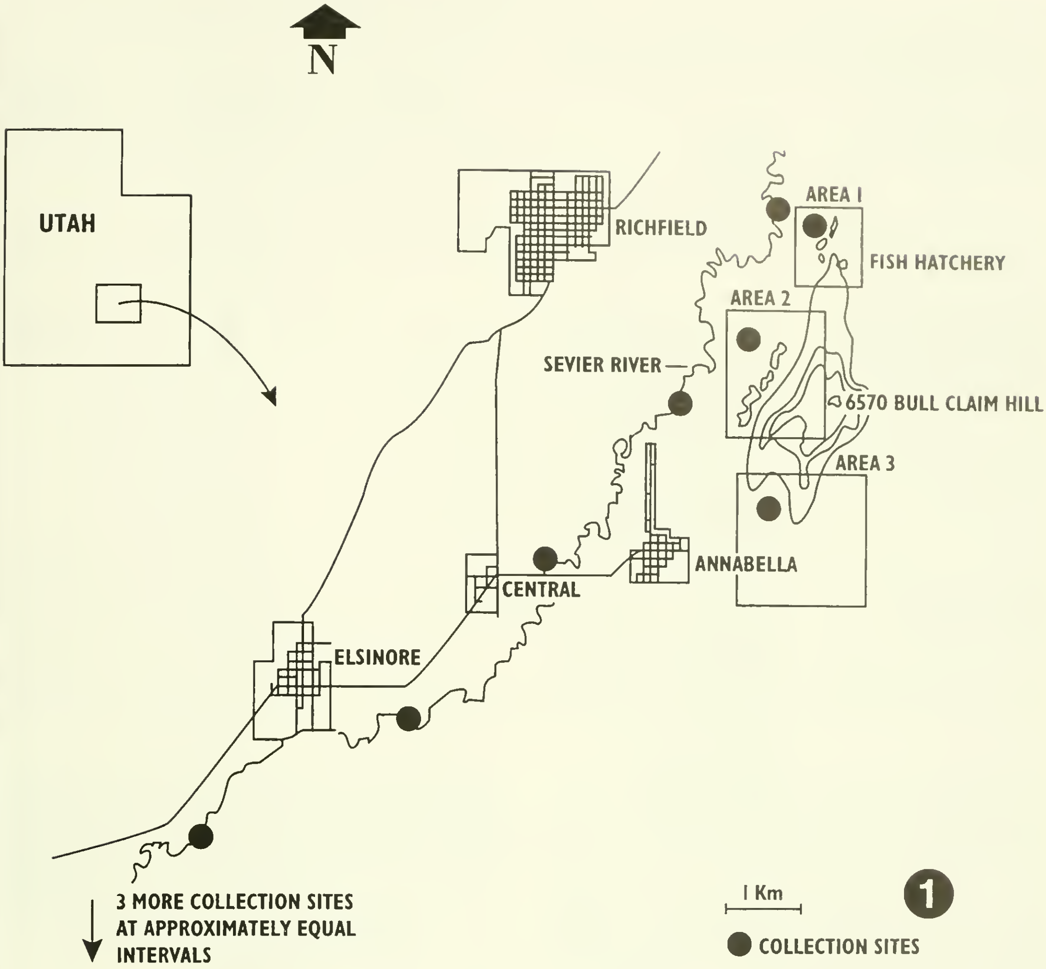
N
UTAH
RICHFIELD
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ANNABELLA
CENTRAL
ELSINORE
3 MORE COLLECTION SITES AT APPROXIMATELY EQUAL INTERVALS
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1
COLLECTION SITES

Fig. 1. Map of the study area near Richfield, Utah, showing collection sites on the Sevier River and location of the spring ponds (areas 1, 2, and 3) near Bull Claim Hill.

Another species, *C.* (=*Trypanoplasma*) *cataractae*, was described by Putz (1972a) from several cyprinids in West Virginia. This record also included the first comprehensive study of a *Cryptobia* (=*Trypanoplasma*) species that encompassed comparative morphology, mode of transmission, natural and experimental hosts, in viro and in vitro culture, histopathology, and cryopreservation. These criteria and extensive comparison with *T. salmositica* from the West Coast were used to justify designation of *T. cataractae* as a valid species.

An ectoparasitic relationship of *Trypanoplasma* on goldfish (*Carassius auratus* [Linnaeus]) maintained in aquaria was recorded by Swezy (1919). Wenrich (1931) also observed the presence of external flagellates on the gills of carp (*Cyprinus carpio* [Linnaeus]) in Pennsylvania. The use of the scientific name *Trypanoplasma* is accurate for these observations (Lom and Dykova 1992). Khan and Noble (1972) and Khan (1991) recently reported on another species of *Cryptobia, C. dahli*.

Involvement of a vector in transmission of *Cryptobia* (=*Trypanoplasma*) was postulated by Mavor (1915). Katz (1951) observed developmental stages of *Cryptobia* from the gut of the leech *Piscicola salmositica* and indicated it as a vector for *C. salmositica*. Subsequent experiments showed conclusively that the leech functioned as a vector in the transfer of *C. salmositica* from fish to fish (Becker and Katz

TABLE 1. Prevalence (%) of *Trypanoplasma* sp. in fish examined from the main Sevier River, northern spring ponds, and southern spring ponds east of Richfield, Utah.

Area	Fish species	Number examined	Positive infections	Percent positive
Main Sevier River	*Gila copei*	10	0	—
	Gila atraria	2	0	—
	Richardsonius balteatus	28	0	—
	Rhinichthys osculus	1	1	100
	Cottus bairdi	1	0	—
	Salmo trutta	2	0	—
Northern spring ponds	*Gila atraria*	20	20	100
	Richardsonius balteatus	20	20	100
	Rhinichthys osculus	20	20	100
	Oncorhynchus mykiss	10	0	—
	Cyprinus carpio	10	0	—
	Catostomus ardens	10	0	—
Southern spring ponds	*Gila atraria*	20	6	30
	Richardsonius balteatus	20	0	—
	Rhinichthys osculus	5	0	—
	Ameiurus melas	2	0	—
Totals—all areas	*Gila copei*	10	0	—
	Gila atraria	42	26	62
	Richardsonius balteatus	68	20	29
	Rhinichthys osculus	26	21	81
	Oncorhynchus mykiss	10	0	—
	Cyprinus carpio	10	0	—
	Catostomus ardens	10	0	—
	Salmo trutta	2	0	—
	Ameiurus melas	2	0	—
	Cottus bairdi	1	0	—

1965a, 1965c, Burreson 1982). Putz (1972b) showed a leech, *Cystobranchus virginicus*, to be a vector for *T. cataractae*.

Organisms of the genus *Cryptobia* and *Trypanoplasma* have been reported as parasites in marine and freshwater fishes, salamanders, frogs, heteropods, planarians, siphonophores, chaetognaths, leeches, mole crickets, lizards, snails, and also as free-living forms (Noble 1968).

Woo and Wehnert (1983) and Bower and Margolis (1983) reported that *Trypanoplasma* and *Cryptobia* of many species of fish can be acquired directly via water and not only by leeches. Bower and Margolis (1984) and Woo (1987) also considered *Trypanoplasma* a synonym of *Cryptobia*, a view not helped by Becker and Katz (1966) or Lom (1979) prior to this time.

The species of *Trypanoplasma* described in this article was first observed by McDaniel in 1970 (personal communication) from Utah chub (*Gila atraria*) near Richfield, Utah. At that time it was considered a species of *Cryptobia*.

MATERIALS AND METHODS

Study Area

The primary collection site, located approximately 5 km east of Richfield, Utah, was subdivided into 3 major areas (Fig. 1): the main Sevier River (area 1), northern spring ponds (area 2), and southern spring ponds (area 3). The ponds are located east of the Sevier River at the base of Bull Claim Hill. The springs are rocky and contain dense stands of watercress and other aquatic plants. The river is heavily silted and almost dry during the summer. Fish were also examined from source waters of a fish hatchery in the northern spring area and from 7 stations on the Sevier River south of the principal study area to determine the local range of the hemoflagellate.

Collection and Examination of Fish

A total of 181 fish representing 5 families and 10 species were collected and examined for blood flagellates (*Trypanoplasma* and *Cryptobia*) using the "kidney strike" technique

TABLE 2. Natural hosts, vectors, and references of *Trypanoplasma* spp. from freshwater fishes of North America.

Species	Vector	Natural hosts (fish)	References
Trypanoplasma atraria sp. n.	*Piscicola salmositica*	*Gila atraria, Richardsonius balteatus, Rhinichthys osculus*	Present study
T. cataractae	*Cystobranchus virginicus*	*Rhinichthys cataractae, Rhinichthys stratulus, Exoglossum maxillingua, Campostoma anomalum*	Putz 1970, 1972a, 1972b
T. salmositica	*Piscicola salmositica*	*Oncorhynchus kisutch, Cottus rhotheus, Cottus aleuticus, Oncorhynchus mykiss, Oncorhynchus tshawytscha, Salmo trutta, Catostomus snyderi, Oncorhynchus keta, Oncorhynchus gorbuscha, Prosopium williamsoni, Cottus bairdi, Cottus gulosus, Cottus beldingi, Cottus perplexus, Cottus asper, Rhinichthys cataractae, Gasterosteus aculeatus*	Katz 1951, Wales and Wolf 1995, Becker and Katz 1965b, 1966, Putz 1972a, 1972b, Becker and Katz 1977
T. gureneyorum	None given	*Coregonus clupeaformis, Salvelinus namaycush, Esox lucius*	Laird 1961
T. borreli	None given	*Catostomus commersoni*	Mavor 1915

(Putz 1970). Hemoflagellates were detected by characteristic whiplike motions of the flagella. Examination of stained preparations at higher magnification confirmed infections and permitted morphological studies.

Collection and Identification of Leeches

Ectoparasitic leeches of fishes were collected from the underside of rocks in the 2 spring areas and identified using Hoffman (1967). Specimens were confirmed by Dr. Roy W. Sawyer, Biology Department, College of Charleston, South Carolina. Leeches were maintained in the laboratory at 4° C in covered paper cups, where they could be kept in good condition for up to 3 mon.

Mounting and Staining

Blood was obtained from the caudal peduncle of infected fishes. Samples of hempoetic tissue were also taken directly from the kidney ("kidney strike"). A thin smear was prepared on a glass slide, air-dried, fixed with methyl alcohol (100%), and stained with Giemsa (Humason 1967).

Stained smears from leeches were prepared by mortaring each leech in a small amount of Hank's balanced salt solution (Hoffman 1967). A smear from the solution was stained following the fish blood procedure. Living *Trypanoplasma* were observed in wet mounts from infected fish and mortared leeches to determine behavioral characteristics.

Morphometrics

Stained slides were examined at a magnification of 1000X. Measurements were recorded for anterior and posterior flagella lengths, body length and width, kinetoplast length, and width of the nucleus. Fifty organisms were measured and averages compared with existing measurements of other described species of *Cryptobia* and *Trypanoplasma*.

RESULTS

Natural Hosts

Examination of 181 fish at 15 stations revealed *Trypanoplasma* in Utah chub (*Gila atraria*), redside shiner (*Richardsonius balteatus*), and speckled dace (*Rhinichthyes osculus*). Seven species (Table 1) appeared to be negative for the blood flagellate: Utah sucker (*Catostomus ardens* [Jordan and Gilbert]), black bullhead (*Ameiurus melas* [Rafinesque]), rainbow trout (*Oncorhynchus mykiss*), brown trout (*Salmo trutta* [Linnaeus]), carp (*Cyprinus*

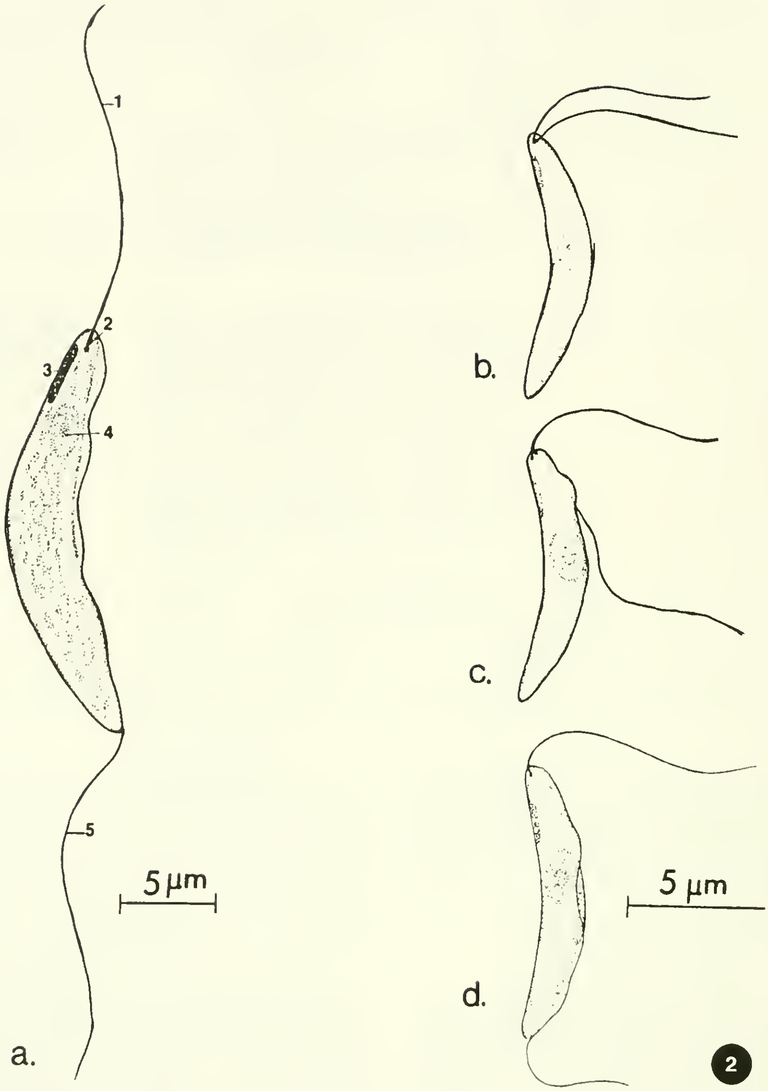

Fig. 2. *Trypanoplasma atraria* sp. n. from fishes (a) and a leech vector (b, c, d): 1, anterior flagellum; 2, blepharoplast; 3, kinetoplast; 4, nucleus; 5, posterior flagellum. (b) Both flagella in anterior position, (c) posterior migration of flagellum, (d) common stage in leech with short posterior flagellum.

capio), leatherside chub (*Gila copei* [Jordan and Gilbert]), and mottled sculpin (*Cottus bairdi* [Girard]). Rainbow trout, carp, and Utah sucker all came from the northern springs ponds (area 2), while the leatherside chub, brown trout, and mottled sculpin were only in the Sevier River. Utah chub and speckled dace were abundant in the springs, but only 2 chub and 1 speckled dace were collected from the Sevier River. The 2 black bullhead were from the southern spring ponds (area 3). Only redside shiner was abundant at all collection sites. Reported natural hosts and vectors of described species of *Trypanoplasma* and *Cryptobia* from North America are given in Table 2.

Prevalence of *Trypanoplasma* in the Richfield, Utah, Area

Fish infected with *Trypanoplasma* were, with 1 exception, obtained in the 2 spring areas along Bull Claim Hill (Table 1). One speckled dace was collected where 1 of the northern springs emptied into the Sevier River. In area 1, all individuals of the 3 host species were infected.

At area 2, the parasite was present in 30% of Utah chub and absent in speckled dace and redside shiner (Table 1). Microscopic examination of kidney fluids from northern spring fishes revealed 3–4 flagellates per field at 100X. For the southern springs, examination of several fields at the same magnification was necessary to locate a single parasite, indicating a much lower level of infection in that area.

Vector

The parasitic leech recovered in the study area was identified as *Piscicola salmositica*, a common ectoparasite of fish in freshwater streams of the West Coast of the United States (Hoffman 1967). Microscopic examination of the mortared leech preparation revealed several developmental stages of *Trypanoplasma*, which were all morphologically different from the parasite stage in the fish (Fig. 2). This correlates with observations by other workers in the field (Lom and Dykova 1992).

Piscicola salmositica was observed from the northern springs ponds and the northernmost portion of the southern area. Extensive search of the remainder of the southern springs and Sevier River produced no additional specimens of the leech. Leech prevalence was high in autumn and continued until peak numbers were observed in the middle of February. By late March to July, only a small number of leeches were observed.

Rainbow trout, carp, Utah sucker, and Utah chub were hosts for *P. salmositica*. Leeches were never observed on redside shiner or speckled dace.

Description of *Trypanoplasma atraria* sp. n.

(Fig. 3)

Average parameters given in micrometers with ranges in parentheses of 50 stained specimens of *Trypanoplasma atraria* sp. n. are as follows: body length 30.5 (27.36), body width 4.5 (3–7), length of anterior flagellum 29.2 (23–34), length of posterior flagellum 20.9 (15–24), nuclear width 2.7 (2–3.5), kinetoplast length 5.9 (4.5–7). Type specimens including paratypes have been deposited (USNM Helminthological Collection Nos. 74436 and 74437), with additional paratypes in the junior author's collections. Morphometric comparisons with other described species of *Trypanoplasma* from North America are shown in Table 3.

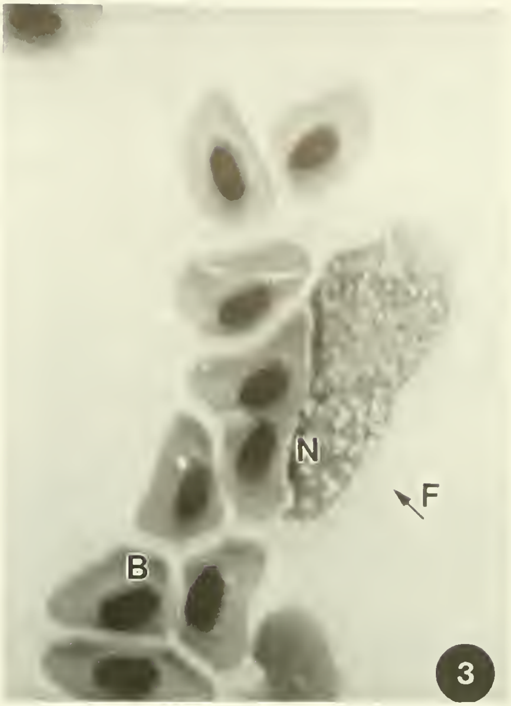

Fig. 3. *Trypanoplasma atraria* sp. n. Note erythrocyte (B), flagella (F), nucleus (N), and body of protozoan; 1000X magnification.

Trypanoplasma atraria sp. n. under phase microscopy revealed a high degree of polymorphism and constant whiplike undulatory movement. Stages in the leech exhibited a qivering motion with much less distortion of body shape. The most common stage visible in the leech had a short posterior flagellum and was less than 1/2 the overall size of that observed from the fish host (Fig. 2d).

DISCUSSION

Published host records for *Trypanoplasma* in North America include 25 species of freshwater fishes (Putz 1972a). *Trypanoplasma salmositica* is reported to parasitize 19 species, *T. cataractae* 4, *T. gurneyorum* 3, and *T. borreli* only a single host species. Results of this study showed *T. atraria* in 3 cyprinids: Utah chub, redside shiner, and speckled dace.

The only known vectors of *Trypanoplasma* are parasitic leeches. Two species have been demonstrated as vectors in North America: *Piscicola salmositica* as a vector of *T. salmositica* (see Becker and Katz 1965a, and

TABLE 3. Morphometric comparison of *Trypanoplasma atraria* sp. n. (ranges in parentheses) with other species of *Trypanoplasma*[a] described from the blood of North American freshwater fishes (all measurements in micrometers).

Species	Total length	Width	Length of anterior flagella	Length of posterior flagella	Nuclear width	Kinetoplast length
Tryanoplasma atraria sp. n.	30.5 (27–36)	4.5 (3–7)	29.1 (23–34)	20.9 (15–24)	2.7 (2.0–3.5)	5.9 (4.5–7.0)
T. cataractae	17	2	11	14	1.0–1.5	2.6–3.1
T. salmositica	14.94	2.46	16.05	8.96	1.5–3.5	4.58
T. gureneyorum	25.1	6.7	19	10	None given	None given
T. borreli	20–25	3–4	None given	None given	None given	None given

[a]There is a close relationship between the two blood flagellates: *Cryptobia* and *Trypanoplasma*. Species of *Trypanoplasma* are transmitted usually by a leech vector.

Cystobranchus virginicus as the vector of *T. cataractae* (see Putz 1972a). The salmonid leech, *Piscicola salmositica*, is probably the hemoflagellate vector in this study. No direct transmission experiments were conducted, but leeches were observed parasitizing fishes at the collection sites, and *Trypanoplasma* was observed in leech guts. The protozoan appears to undergo developmental changes within the leech with the trailing flagellum migrating anterior to posterior and forming the undulating membrane (Fig. 2). The size of the flagellate in the leech was about 1/3 to 1/2 that of the parasite in the fish host. Becker and Katz (165a) reported *P. salmositica* as endemic to the Pacific Coast of North America. Cope (1958) and Heckmann (1971) identified salmonid leeches from cutthroat trout in Yellowstone Lake. Direct transmission studies would clarify the role of the leech relative to fish infections with *T. atraria*.

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GEOGRAPHICAL REVIEW OF THE HISTORICAL AND CURRENT STATUS OF OSPREYS (*PANDION HALIAETUS*) IN UTAH

Clark S. Monson[1]

ABSTRACT.—Small numbers of Ospreys (*Pandion haliaetus*) are known to have nested historically in Utah. A precise baseline figure is unavailable, but the 19th-century Osprey population in Utah probably consisted of at least 15 breeding pairs scattered in 4 geographic regions. Human persecution is believed to have caused the abandonment of nesting territories along the Wasatch Front and in the western Uinta Mountains by 1900 and 1960, respectively. Osprey populations in the southern plateaus and Green River areas, however, began increasing in the late 1970s. Several recent nesting attempts and numerous summer sightings at nontraditional and abandoned historical sites in Utah suggest the Osprey is also expanding its range in Utah. High productivity for local pairs and long-range dispersal from more northerly Osprey populations are discussed as sources for the current surge in Utah's Osprey population, which now consists of approximately 35 breeding pairs.

Key words: Osprey, Pandion haliaetus, *raptor, Flaming Gorge Reservoir, dispersal.*

The Osprey (*Pandion haliaetus*) is one of the most widely distributed species of raptors during the breeding period. The extent of its cosmopolitan range is exceeded by only 2 other raptors: the Peregrine Falcon (*Falco peregrinus*) (Cade 1982, del Hoyo et al. 1994) and Barn Owl (*Tyto alba*) (Marti 1985, Eckert and Karalus 1987). Despite the Osprey's broad geographic distribution, local populations occur in fragmented and low densities in much of the species' range (Bent 1937, Palmer 1988, del Hoyo et al. 1994). This scenario holds true for most of the intermountain region of the western United States (Henny 1986, Johnsgard 1990). In Utah, Osprey distribution has been particularly limited. Recently, however, several personal summer observations of Ospreys over 140 km from known breeding pairs prompted an investigation into the possible occurrence of Ospreys at other nontraditional Utah localities.

A survey of individuals from the U.S. Forest Service, Utah Division of Wildlife Resources, Utah State Parks, and other persons familiar with Osprey ecology was conducted during 1994–95. The survey revealed many Osprey sightings and several nesting attempts between 1 June and 15 August at numerous lakes, reservoirs, and rivers from nearly every region of the state since 1990. These sightings represent the first widespread effort by Ospreys to expand their range in Utah. This paper reviews historical Osprey breeding territories in Utah, subsequent population declines, and current Osprey population and range expansion in Utah.

GEOGRAPHIC HISTORY OF THE OSPREY IN UTAH

Nesting Ospreys have been reported from 4 geographical areas of Utah (Fig. 1): the Wasatch Front, Uinta Mountains, southern plateaus, and Green River (Table 1). Accounts of early ornithologists, naturalists, and egg collectors indicate the Osprey was a regular summer resident and breeder in Utah. Allen (1872) found them along the Great Salt Lake marshes west of Ogden, and Henshaw (1874) saw them at Utah Lake near Provo. Neither discussed nest observations in these areas, but R. G. Bee (unpublished ornithological notes) mentioned that Ospreys formerly nested along the shores and tributaries of Utah Lake (Fig. 1; Table 1, region A).

Other records were for the Uinta Mountains (Fig. 1; Table 1, region B). J. D. Daynes (unpublished ornithological notes) described the repeated use of an Osprey nest from 1915 to 1938 on the Weber River, 20 km east of Oakley, Summit County. Also, Hayward (1931)

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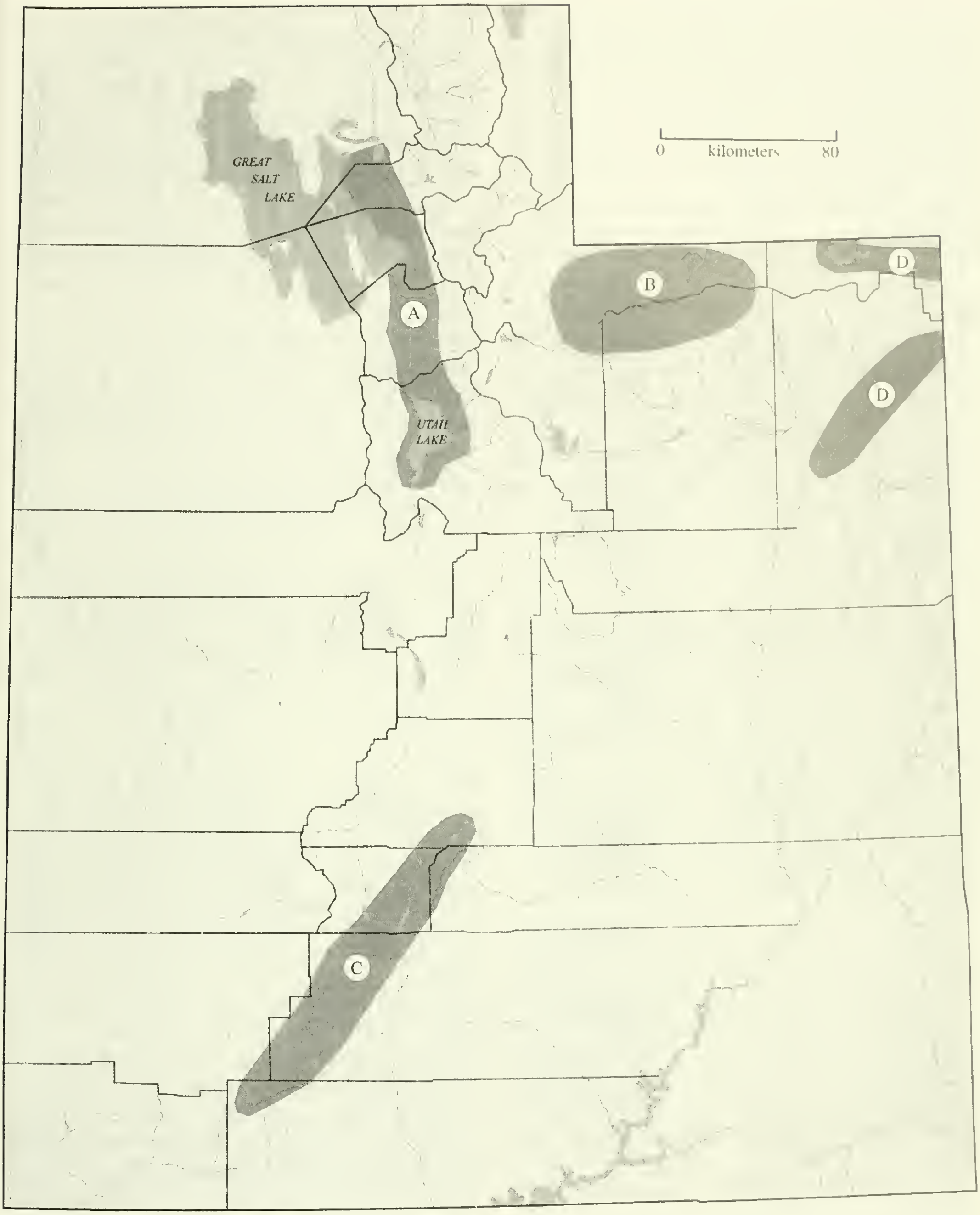

Fig. 1. Known historical distribution of nesting Ospreys in Utah: A, Wasatch Front; B, western Uinta Mountains; C, southern plateaus; D, Green River.

surveyed (8 July–21 August 1930) birds in the western Uintas where Summit, Duchesne, and Wasatch counties converge. While not giving actual locations, he said a few Ospreys nested in the Mirror and Tryol [*sic*] lakes region. Bee and Hutchings (1942) specifically cite Mirror and Trial lakes as having Osprey nests. Twomey (1942: 382) visited an occupied nest between 16 and 20 July 1932 at the north end of Mirror Lake, "Wasatch County." This nest was actually

TABLE 1. Nesting populations of Ospreys in Utah.

Region	Historical pairs	Current pairs
A: Wasatch Front	Unknown	1
B: Uinta Mountins	5–8	0
C: Southern plateaus	2–4	8–11
D: Green River	6–8	20–25

in Duchesne County and perhaps the same nest Hayward et al. (1976) referred to when they listed Wasatch County as a former nesting area. R. G. Bee (unpublished ornithological notes) also cited single pairs at Fish, Scout, and Lily lakes in the western Uintas. On 23 May 1945, Bee recorded that a game warden in Duchesne informed him of 2 pairs at Moon Lake and another pair at an unidentified Uinta lake.

Other early observers of Osprey nests in Utah include Wolfe and Cottam (Hayward et al. 1976), who, along with Bee and Hutchings (1942), saw Ospreys nest at Fish Lake (not the Uinta Mountains lake with the same name), Sevier County, beginning in 1928 (Fig. 1; Table 1, region C). On 18 July 1936, R. G. Bee (unpublished ornithological notes) visited the Fish Lake nest. A local rancher told him Ospreys had used that particular nesting site for at least 20 years.

Behle et al. (1958) noted a pair of Ospreys in southwestern Utah at Navajo Lake, Kane County, on 17 and 18 June 1950 (Fig. 1; Table 1, region C). This particular territory (and an additional site at nearby Panguitch Lake, Garfield County) has been used regularly since Behle's discovery (Eyre and Paul 1973, *Salt Lake Tribune*, 13 August 1978, Walters 1981, Anonymous 1989).

Ospreys also nested along the Green River, northeastern Utah (Fig. 1; Table 1, region D). On 23 and 24 July 1959, C. M. White and C. Bosley (White and Behle 1960) located 2 nests along this river in Horseshoe Canyon, Daggett County. Both nests contained 2 young. An additional nest was discovered on the Green River in Uintah County by M. Horton in June 1974 (Behle 1981). White (1969) suggested the total population of Ospreys nesting along the Green River probably consisted of 6–8 pairs.

STATUS

Historical Events

Although numerous records of Ospreys nesting in Utah exist, these birds have apparently undergone 2 separate declines. The 1st decline involved Ospreys nesting along the Wasatch Front (Fig. 1). During winter 1848–49, depredations upon livestock, poultry, and grain led to a much-publicized contest to kill the "wasters and destroyers" (Arrington 1958: 51). Hundreds of mammalian predators and thousands of raptors were killed (Arrington 1958). Ospreys would have been on their southern wintering grounds during this assault on local predators, but the incident suggests that early pioneers in Utah treated all carnivores and birds of prey with contempt. Other similar hunts followed, and 40 years later the Utah Legislature implemented a law awarding bounties for the killing of predators (Rawley 1985). Rewards were available for several species of fish-eating birds including Ospreys. The destruction that this bounty inflicted upon fish-eating birds in the name of "conservation" was significant and is vividly described by Pritchett et al. (1981).

The attitudes of early residents toward predators, coupled with laws encouraging their destruction, may have led to the Osprey's extirpation from the Wasatch Front (Fig. 1; Table 1, region A) around the turn of the century. In 1935, R. G. Bee (unpublished ornithological notes) speculated that human persecution caused the abandonment of Osprey nests near Utah Lake. Bee did not record when these Ospreys disappeared, but his manner of reflection on their absence suggests the loss occurred well before his 1935 notation.

The 2nd period of Osprey decline occurred in the western Uinta Mountains (Fig. 1). The Uinta Mountain nests that Daynes, Bee, Hayward, and Twomey reported were observed before, but apparently not after, the 1950s and 1960s when Osprey colonies along the eastern seaboard were decimated by organochlorine compounds (Palmer 1988, Poole 1989). Although the impact of synthetic agricultural biocides upon Ospreys in Utah is unknown, Ospreys in other areas of the western United States were generally less affected by environmental contaminants than eastern populations (Poole 1989, White 1994).

Another possible reason for the decline of Ospreys in the Uinta Mountains is indiscriminate shooting resulting from a hostile attitude by local residents (Bee unpublished ornithological notes, Twomey 1942). Many Ospreys were formerly shot at northern Utah fish hatcheries during spring migrations (White 1969, Hayward et al. 1976), and some of these casualties could have been local breeders.

Hayward et al. (1976: 66) recorded the Osprey was "formerly a sparse but regular summer resident in Utah; now greatly reduced in numbers and considered to be rare and endangered." They preface their discussion of birds in Utah by stating they have included all records concerning rare species in the state. However, they cited Ospreys only in the western Uintas and records for Fish Lake in Sevier County. They did not include information on the 1 or 2 pairs nesting in the Navajo Lake–Panguitch Lake area, southern Utah, or the pairs at Flaming Gorge Reservoir, northeastern Utah. In the same year (1976) that Hayward et al. (1976: 66) described the Osprey as "greatly reduced," more Ospreys (6 pairs) nested at Flaming Gorge Reservoir (Wagner 1977, *Salt Lake Tribune*, 13 August 1978) than had been recorded in any particular year in the western Uinta Mountains.

Current Events

Flaming Gorge Dam on the Green River was completed in 1964 and created a narrow, 150-km-long reservoir on the Utah-Wyoming border. The Osprey population here remained relatively stable until the late 1970s and 1980s when an increase was noted (Behle 1981). Crawley and White (1989) found 21 pairs and 1 trio of Ospreys at Flaming Gorge in 1989. Of these, 15 pairs succeeded in fledging 37 young.

Osprey numbers at Fish Lake in Sevier County increased from 2 pairs in 1989 (Anonymous 1989) to 6 in 1993 (B. Lowry, U.S. Forest Service, personal communication). Additionally, 1 or 2 pairs now nest 3 km away at Johnson Valley Reservoir (P. Wagner personal communication). Other current Osprey nest sites at traditional waters in Utah include 2 pairs in the Panguitch Lake–Navajo Lake area of southern Utah (Anonymous 1989).

In 1990 a pair of Ospreys nested at Tropic Reservoir, Garfield County (Sorensen 1990). This site is 20 km east of region C (Fig. 1, Table 1) and should be regarded as a geographical extension of that area. In 1994 a pair of Ospreys constructed a nest near the Midway fish hatchery, Wasatch County (Fig. 2A). In 1995 a 2nd pair built a nest 2 km away at Deer Creek Reservoir on a 5-m-high artificial platform erected for Ospreys (Fig. 2B). Deer Creek Reservoir and the adjacent Midway fish hatchery have been frequented by Ospreys during spring migrations for many years (Behle and Perry 1975). Additional Osprey nesting attempts in 1995 include 1 pair at Jordanelle Reservoir, Wasatch County (Fig. 2C), and another pair near Highland, Utah County (Fig. 2D). Incubation behavior at the latter site was observed for approximately 2 wk before strong winds destroyed the nest. This site was possibly the first Osprey nest along the Wasatch Front in 80–100 yr.

The origin of Ospreys colonizing new waters in Utah is currently unknown, but their reluctance to disperse more than 125 km from their natal sites is well documented (Henny 1986, Poole 1989). Reproduction for nests at Flaming Gorge Reservoir is generally high (Crawley and White 1989), and considering the Osprey's pronounced philopatry, one might expect that Ospreys at new locations in Utah derive from this local population. While high productivity has augmented the Osprey population on Flaming Gorge, the frequency with which Ospreys are being witnessed in Utah is too great to be the sole result of dispersal from that reservoir. Moreover, if Flaming Gorge were the primary source of Ospreys pioneering new waters in Utah, one would expect lakes and rivers near that reservoir to be the initial areas of range expansion. This has not been the case.

A more plausible source of Ospreys attempting to colonize nontraditional (and abandoned historical) waters in Utah is from spring migrants stopping short of their natal territories farther north. Osprey populations in Idaho and Wyoming number in the hundreds of pairs (Henny 1986, Poole 1989), and Osprey counts made at several migration points in the West have burgeoned since 1983 (Hoffman et al. 1992). Furthermore, migrating subadult Ospreys are known to linger sometimes and even remain at productive foraging sites south of their traditional breeding grounds (Swenson 1981, Poole 1989). These lingering individuals may represent young adults without an established history of breeding elsewhere.

If more northerly populations constitute the primary source of Ospreys currently pioneering nontraditional waters in Utah, this long-

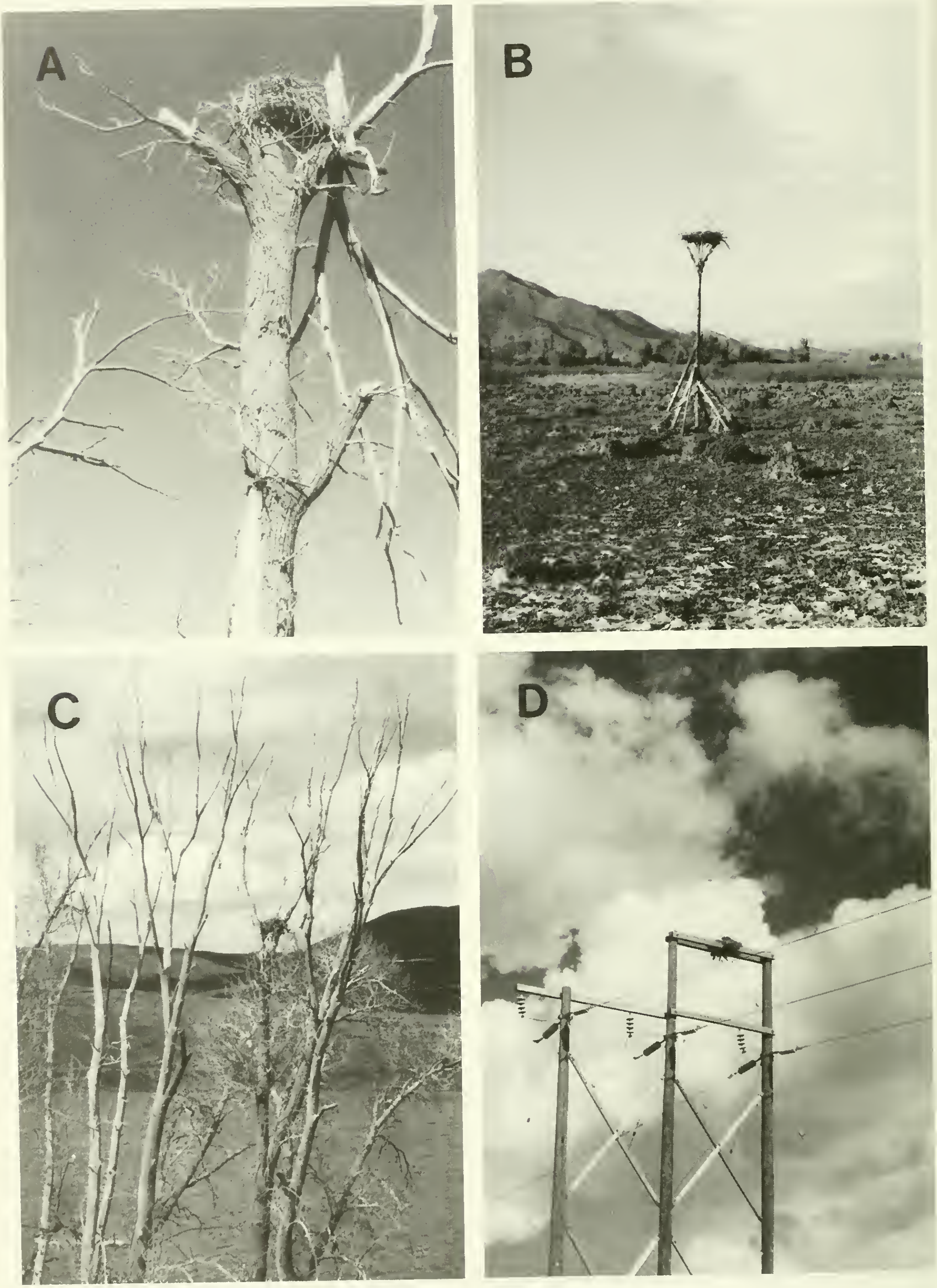

Fig. 2. A, Osprey nest, Midway fish hatchery; B, Osprey nesting platform and nest, Deer Creek Reservoir; C, Osprey nest, Jordanelle Reservoir; D, Osprey nest and incubating adult near Highland, Utah.

distance dispersal is a recent phenomenon and possibly indicates a saturated breeding population in the northern Intermountain West. A current, quantitative evaluation of Osprey populations in Idaho and Wyoming and extensive banding efforts in these states could help determine if this speculation is correct. Until such a project is undertaken, the origin of Ospreys presently colonizing new waters in Utah is open to conjecture.

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EFFECTS OF TURBIDITY ON FEEDING RATES OF LAHONTAN CUTTHROAT TROUT (*ONCORHYNCHUS CLARKI HENSHAWI*) AND LAHONTAN REDSIDE SHINER (*RICHARDSONIUS EGREGIUS*)

Gary L. Vinyard[1] and Andy C. Yuan[1]

ABSTRACT.—The spawning population of Lahontan cutthroat trout (*Oncorhynchus clarki henshawi*) in Summit Lake, Nevada, has reportedly declined since the early 1970s, coincident with the appearance of Lahontan redside shiner (*Richardsonius egregius*) in the lake. We investigated the relative predatory abilities of these 2 fish species foraging on live *Daphnia magna* in turbidity conditions commonly observed in Summit Lake. Experiments were performed under controlled light and temperature conditions. In separate trials we fed trout and shiner 1 of 3 size classes of *D. magna* (1.7 mm, 2.2 mm, and 3.0 mm) at 6 levels of turbidity ranging from 3.5 to 25 NTU. Feeding rates for both species varied inversely with turbidity for all prey sizes. Feeding rates of shiner were greater than trout at all turbidity levels. In low turbidity (5 NTU), shiner consumed approximately 3% more prey during 2-h feeding trials. However, at high turbidity levels, the difference in feeding rates between species was proportionally higher (10%). At high turbidity levels (≥ 20 NTU) trout predation rates were relatively insensitive to prey size. However, shiner continued to consume more, larger prey at the highest turbidity levels. These results indicate that Lahontan redside shiner may be superior to Lahontan cutthroat trout as zooplankton predators at high turbidity levels, and may explain the recent success of shiner in Summit Lake.

Key words: Daphnia, *Lahontan cutthroat trout,* Oncorhynchus clarki henshawi, *Lahontan redside shiner,* Richardsonius egregius, *planktivory, predation, size selectivity, turbidity.*

The Lahontan cutthroat trout (*Oncorhynchus clarki henshawi*) is an inland subspecies endemic to the physiographic Lahontan basin in northern Nevada, eastern California, and southern Oregon. These trout were once widespread throughout the basins of Pleistocene Lake Lahontan (USFWS 1995). Currently, they occupy <1% of their former lacustrine range and 11% of their former stream habitat within the native range (USFWS 1995). Listed as endangered in 1970, the fish was subsequently reclassified as threatened in 1975. This facilitated management and permitted regulated angling (USFWS 1995).

Summit Lake is located in the Summit Lake Paiute Indian Reservation in northwestern Humboldt County, Nevada (41°N latitude 119°W longitude), at an elevation of 1828 m. Formed by a landslide about 20,000 years ago, Summit Lake is relatively shallow (maximum depth 12 m) and has historically been subject to high turbidity levels during summer months from suspended algae and silt (LaRivers 1962). It contains the most secure remaining lacustrine population of Lahontan cutthroat trout, and no other salmonids occur in the basin (Cowan and Blake 1989, Valeska 1989). Other lacustrine populations are either maintained by artificial stocking or are subject to higher levels of harvest and disturbance. Conservation of this population is compelling, and it has been identified as important for recovery of the subspecies (USFWS 1995).

Cutthroat trout spawning runs at Summit Lake have generally declined since the late 1970s (Cowan and Blake 1989). Collection of roe during the 1960s and 1970s and excessive loss of spawning habitat in Mahogany Creek from livestock overgrazing (Cowan and Blake 1989, Vinyard and Winzeler 1993) have been blamed. However, coinciding with the decline in trout, Lahontan redside shiner (*Richardsonius egregius*) also increased in abundance in the lake, suggesting a competition effect.

Redside shiner are native to the Great Basin, but they do not occur naturally in Summit Lake. Origins of the present shiner population in the lake are unknown, but they have been used frequently as live bait. Lahontan redside shiner feed on drift in streams and are zooplanktivorous in lakes (Vinyard and Winzeler 1993). Laboratory observations suggest they may also prey on larval trout (Vinyard and Winzeler 1993). Analysis of stomach contents suggests that Lahontan cutthroat trout and Lahontan redside shiner probably consume similar foods both in Summit Lake and in Mahogany Creek, the primary spawning tributary for trout from Summit Lake (Vinyard and Winzeler 1993). Both species consume drift in the stream, and mostly amphipods in Summit Lake (Cowan and Blake 1989). In contrast, similarly large Lahontan cutthroat trout in Pyramid Lake are piscivorous (USFWS 1995). Because most fish species depend on vision to locate prey (Hobson 1979, Guthrie 1986), it is possible that high turbidity in Summit Lake limits the visibility of prey and impedes the ability of trout to catch redside shiner and other large prey.

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Our experiments compared the relationships of feeding rate, turbidity, and prey size for Lahontan cutthroat trout and Lahontan redside shiner, with the primary focus being to examine the relative performance of both species under various turbidity levels.

METHODS AND MATERIALS

Lahontan redside shiner were captured from Mahogany Creek, Humboldt County, Nevada, and transported to the University of Nevada. Lahontan cutthroat trout from the current Pyramid Lake stock were acquired from the Lahontan National Fish Hatchery, Gardnerville, Nevada. Although the historical origins of the existing Pyramid Lake stock are mixed, Summit Lake fish were heavily planted into Pyramid Lake for a number of years, and they likely constitute the dominant component of the population (USFWS 1995). Fish were housed in 19-L tanks and acclimated to local water conditions for at least 3 wk prior to experiments.

Experiments were conducted in a secluded section of a greenhouse at the University of Nevada. The experimental protocol was similar to that employed by Vinyard and Winzeler (1993) and Li et al. (1985). Visual isolation of experimental tanks was ensured by opaque black polyethylene sheeting (10 mil, 2.5 m high), which enclosed all sides of the experimental area and controlled external light. Temperatures ranged between 12°C and 17°C during the experiments, and diel variation never exceeded 4°C, a range easily tolerated by both species. Lighting was provided by a bank of three 56-watt fluorescent tubes controlled by an automatic timer (10L:14D). Light intensity at the water surface averaged 93 μE m^{-2} S^{-1}. An airstone in the center of each of four 38-L aquaria provided aeration and kept turbidity in suspension. Turbidity (nephelometric turbidity units, NTU) was measured with an HF Instruments Model DRT 15 turbidimeter. Six turbidity levels (3.5, 6, 10, 20, 22, and 25 NTU) were produced using suspensions of bentonite. Bentonite concentrations (mg/L) were significantly correlated with measured turbidity (NTU = 2.583 + 0.162 B, r^2 = 0.99). This material is nontoxic and remains in suspension for long periods.

Feeding rates were determined for fish exposed to single-sized groups of *Daphnia magna* at each turbidity level. Laboratory-reared *D. magna* were sorted into 3 size groups using a dissecting microscope: 1.7 mm, 2.2 mm, and 3.0 mm (top of head to base of tail spine, ± 0.3 mm). Before each feeding trial, a single fish was placed into each experimental tank and allowed to acclimate for 24 h. A group of 200 *Daphnia* were introduced into the tank and the fish allowed to feed for 2 h. Fish were then removed and the water and remaining prey siphoned through a 363-micron mesh net. Prey retained on the net were counted to determine consumption rates. This procedure was repeated for each of the 3 prey size classes and 6 turbidity levels with 4 fish from each species, yielding a total of 144 feeding trials. Fish used in the feeding trials ranged from 70 mm to 93 mm SL. Analysis of variance and linear regression were used to assess the effects of fish species, prey size, and turbidity level on predation rates.

RESULTS

An analysis of overall predation rates for both fish species consuming all prey sizes (Figs. 1a, 1b) indicates that feeding rates varied inversely with turbidity (multiple regression, F = 1894, $P < 0.001$) and between fish species (F = 28.4, $P < 0.001$), and that larger prey generally were consumed at greater rates (F = 38.3, $P < 0.001$). Significant results were observed for both the species*NTU and species*daphnia size interaction terms, indicating that the 2 fish species differ in their responses to these 2 variables. Lahontan redside shiner consumed significantly more prey than Lahontan cutthroat trout. At the lowest turbidity level (3.5 NTU), approximately 90% of all prey were consumed by both fish species. However, even small increases in turbidity reduced predation rates. This decrease in predation with turbidity was strongly linear, and there was no indication of a minimum value having been reached by 25 NTU. At that turbidity level, predation rates declined by approximately 80% for trout (Fig. 1a) and by 60% to 80% for shiner (Fig. 1b), depending on prey size. Predation rates for trout were significantly affected by prey size and turbidity (multiple regression $F = 2.67$, $P = 0.009$ for prey size; $F = 35.1$, $P < 0.001$ for turbidity). Similar results were observed for shiner (multiple regression $F = 6.54$, $P < 0.001$ for prey size; $F = 27.15$, $P < 0.001$ for turbidity).

At higher turbidity levels, differences in performance of the 2 fish species became most apparent. At turbidity levels of 20 NTU or more, prey of all sizes were consumed at virtually equal rates by Lahontan cutthroat trout (Fig. 1a). In contrast, Lahontan redside shiner showed increasing predation on 3-mm prey relative to the smaller sizes at high turbidity levels (Fig. 1b), and shiner showed the greatest differences in predation rates between prey of different size at the highest turbidity levels. Lahontan cutthroat trout exhibited the opposite trend, with greater differences in predation rates between prey of different sizes at low turbidity levels.

DISCUSSION

Foraging behavior and efficiency are affected by local visibility. Many workers have demonstrated reduced effectiveness by visual predators at elevated turbidity (Vinyard and O'Brien 1976, Li et al. 1985, Barrett et al. 1992, Gregory and Northcote 1993). Sigler et al. (1984) found that chronic high turbidity impedes growth and increases mortality of steelhead (*O. mykiss*) and coho salmon (*O. kisutch*). Evidence suggests that high turbidity or low light intensity reduces predator selectivity because relative differences in prey-detection distance for different sizes of prey are reduced (Vinyard and O'Brien 1976, Gregory and Northcote 1993). Gregory and Northcote (1993) observed log-linear declines in reactive distance with increased turbidity in chinook salmon (*O. tshawytscha*).

Our results demonstrate that turbidity reduces predation rates for all prey sizes for both Lahontan redside shiner and Lahontan cutthroat trout. Larger prey were generally consumed with greater frequency, although this frequency varies with turbidity and fish species. The effect of prey size was most consistent for Lahontan redside shiner. These fish consumed more large (3.0 mm) prey at all turbidity levels than did Lahontan cutthroat trout (Figs. 1a, 1b). In contrast, prey size had little effect on the relative numbers of prey of each size consumed by trout at turbidity levels of 20 NTU or above (Fig. 1a).

Redside shiner also consumed more prey of all 3 sizes combined over all turbidity levels. For all prey sizes combined, shiner consumed approximately 3% more prey than Lahontan cutthroat trout at low turbidity levels and approximately 10% more at high levels (Figs. 1a, 1b). Angradi and Griffith (1990) found predation by rainbow trout (*O. mykiss*) to be more selective for large prey in clear water, whereas selectivity was reduced in elevated turbidity. Similar effects on prey selection under reduced visibility conditions have been observed in bluegill sunfish (*Lepomis macrochirus*). Under low-light conditions bluegill sunfish consumed fewer zooplankton but proportionally more large individuals (Miner and Stein 1993).

Neither trout nor shiner have been shown explicitly to possess adaptations that might enhance their effectiveness as foragers in turbid waters. However, fish that feed nocturnally, such as walleye (*Stizostedion vitreum*), may perform equally well in either clear or turbid waters (Vandenbyllaardt et al. 1991). Walleye have higher densities of retinal cells and also develop scotopic vision earlier in life in comparison to salmonids (Vandenbyllaardt et al. 1991, Borgstrom et al. 1992, Hurber and Rylander 1992). Such species-specific factors may contribute to differences in visual performance.

Behavioral responses of fish to turbidity may also affect their feeding abilities or rates. In laboratory experiments, golden shiner (*Notemigonus crysoleucas*) showed increased flight responses with increased turbidity (Chiasson 1993). Juvenile chinook salmon apparently experienced reduced predation from piscivorous birds and fishes at elevated turbidity levels (Gregory 1993). During our experiments, redside shiner were observed to search faster

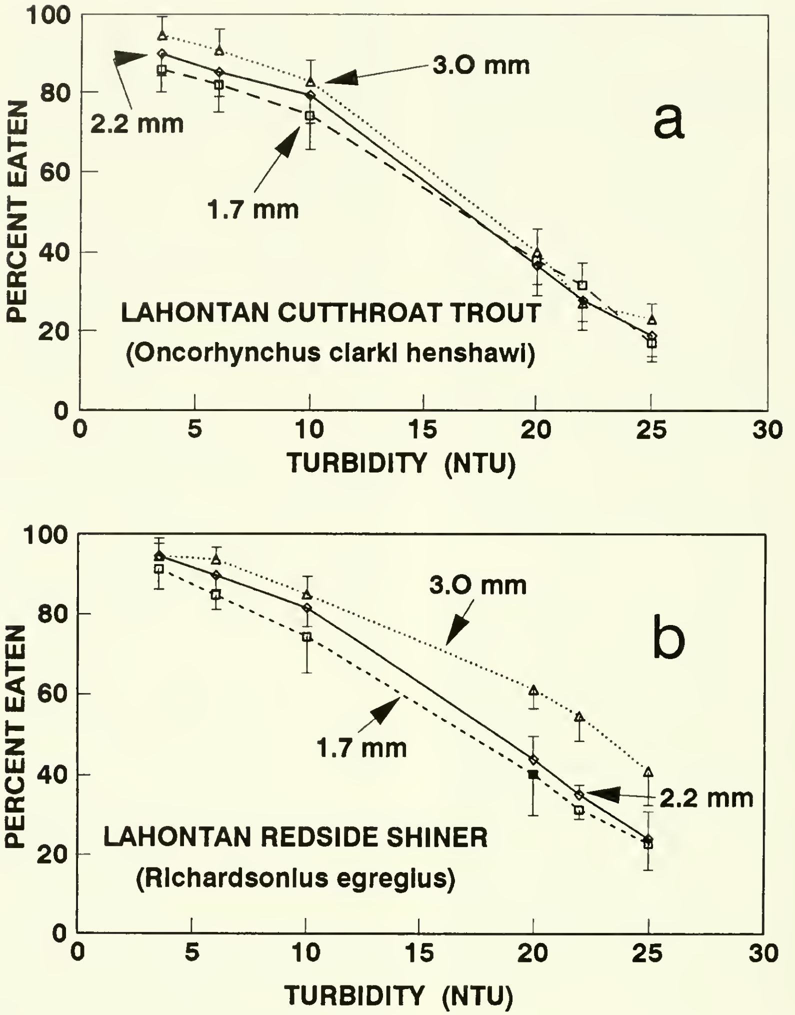

Fig. 1. Mean percent prey consumed in relation to turbidity. Upper panel (a) shows results from feeding trials with Lahontan cutthroat trout (*Oncorhynchus clarki henshawi*), and lower panel (b) shows results from Lahontan redside shiner (*Richardsonius egregius*). Four fish of each species were exposed to prey of a single size for 2-h feeding trials. *Daphnia magna* prey sizes are as indicated. Vertical bars indicate 1 standard deviation.

and more widely at higher turbidity. Elevated turbidity may have provided greater visual isolation and promoted greater mobility by predators as suggested by Confer et al. (1978) and Gradall and Swenson (1982). Increased activity may have compensated for reduced visual effectiveness, resulting in larger search volumes for shiner than for trout. In a study of brook trout (*Salvelinus fontinalis*) and creek chub (*Semotilus atromaculatus*), Gradall and Swenson (1982) found creek chub to be less affected by turbidity than brook trout. They suggested such differential effects may explain local disparities in fish density.

High turbidity in Summit Lake may decrease reactive distance and search volume unequally for shiner and trout. This may differentially reduce the probability of successful prey capture and could produce altered prey selection patterns under different turbidity conditions. Although our results are generally similar to those shown for other fishes (Vinyard and O'Brien 1976, Berg and Northcote 1985, Li et al. 1985), we document highly significant differences between potentially competing fish species. Because Lahontan cutthroat trout and Lahontan redside shiner consume the same prey in Summit Lake, competition for food may exist. Our results suggest that in elevated turbidity conditions Lahontan redside shiner may be a better competitor for food than Lahontan cutthroat trout. A factor contributing to the success of Lahontan redside shiner in Summit Lake may be that their predation rates are higher than those of cutthroat trout at elevated turbidity levels.

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POGONOMYRMEX OWYHEEI NEST SITE DENSITY AND SIZE ON A MINIMALLY IMPACTED SITE IN CENTRAL OREGON

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ABSTRACT.—Little is known about the basic characteristics of the western harvester ant (*Pogonomyrmex owyheei*) in the absence of anthropogenic disturbances. We examined the role of *P. owyheei* as an agent of disturbance in an area of semiarid vegetation in central Oregon known as the Horse Ridge Research Natural Area (HRRNA) that has been largely free of livestock grazing and other significant anthropogenic influences for over 23 yr. We determined density and size characteristics of nest sites and estimated total area cleared by *P. owyheei* activities on HRRNA. From random sampling of twenty-five 0.04-ha plots we found a mean nest density/standard error of 1.6 (±0.16) nests/0.04 ha. Mean area cleared per nest site was 4.8 m^2, which results in an estimated barren area of 46,080 m^2 on the 240-ha HRRNA. Comparing our findings to others on *P. owyheei* and *P. occidentalis*, we found nest density and mean cleared area to be in the middle range of reported observations under a variety of land-use influences. The literature suggests that moderate disturbance may increase nest site density, but little relationship exists between disturbance history and mean size of nest sites.

Key words: Pogonomyrmex owyheei, *western harvester ants, nest density, nest size, vegetation clearing.*

Western harvester ants are a major component of arid rangeland ecosystems in the United States. Because of the combined effects of seed predation, seed dispersal, and vegetation removal, harvester ants are "keystone species," meaning their effects on vegetation structure and dynamics exceed expectations given their density and biomass (Holldobler and Wilson 1990: 616). The most visible impact of harvester ant activities is vegetation clearing around their nest sites. Although the size of the cleared area, or disc, varies, *Pogonomyrmex* harvester ants have the capacity to cut annual plants surrounding their nest sites at rates of over 200 million plants/ha/yr (Clark and Comanor 1975). While much of the plant biomass cut is not consumed by the ants, it reduces the total volume available for consumption by livestock and other grazers (Willard and Crowell 1965). Range managers have viewed *Pogonomyrmex* as pests that need to be controlled, giving the ant both economic and ecological importance in arid rangelands (Wight and Nichols 1966, Cole 1968).

Because of the paucity of undisturbed areas in the semiarid West, little is known about the basic characteristic of *P. owyheei* nest sites in the absence of anthropogenic disturbances. The primary objectives of this study are (1) to determine the density and size characteristics of *P. owyheei* nest sites and (2) to estimate the total area denuded by clearing and foraging activities of *P. owyheei* within a largely undisturbed semiarid ecosystem.

STUDY AREA

The Horse Ridge Research Natural Area (HRRNA) is a 240-ha exclosure 31 km southeast of Bend, Oregon, managed by the Prineville District, Bureau of Land Management (BLM). The natural area was established in 1967, and a surrounding fence was completed in 1974. The exclosure ranges from 1250 to 1430 m elevation over rolling topography of Columbia Basalts (Anonymous 1972). Direct human impacts on the site are minimal as there is only occasional use by hunters and naturalists, and fire suppression is not active (Halvorson 1991, R. Halvorson personal communication 1995). The fence has kept the area free of livestock grazing since 1974, but before its establishment the area apparently received minimal domestic animal grazing pressure because of a lack of a permanent water source to attract animals (Anonymous 1972) and the distance from well-traveled public roads (Baldwin 1974). Additionally, the abundance on HRRNA of threadleaved sedge (*Carex filifolia*), a species that has been shown to decline

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because of overgrazing in the central Oregon sagebrush steppe, and the absence of cheatgrass (*Bromus tectorum*) suggest a minimally disturbed site (Anonymous 1972, personal observation 1995).

Vegetation on HRRNA is classified as the western juniper/big sagebrush/threadleaved sedge community (*Juniperus occidentalis*/*Artemisia tridentata*/*Carex filifolia*) (Franklin and Dyrness 1988). Less common but present species are bluebunch wheatgrass (*Agropyron spicatum*), Idaho fescue (*Festuca idahoensis*), junegrass (*Koeleria cristata*), and horsebrush (*Tetradymia glabrata*) (Anonymous 1972).

HRRNA climate is dominated by winter precipitation. Over half the annual 31 cm falls as snow. Mean temperatures at Bend range from –0.6°C in January to 17.7°C in July (Karl et al. 1990).

Soils on our study plots are entirely within the Stookmoor-Wesbutte complex soil series (USDA-NRCS in press). This soil series is found on approximately 85% of HRRNA. A typical soil profile is represented by a surface layer of mixed ash and loamy material approximately 15 cm thick, and a pale brown, sandy loam subsoil 46 cm deep overlying bedrock. Percentage of organic matter in the topsoil is 1%–2% and 0.5%–2% in the subsoil (USDA-NRCS in press).

Besides *P. owyheei*, there is disturbance pressure on HRRNA from grazing activities of herbivores and granivores such as Rocky Mountain mule deer (*Odocoileus hemionus hemionus*), badger (*Taxidea taxus*), and cottontail rabbits (*Sylvilagus nutalli*) (Gashwiler 1972, personal observation 1995). BLM records on HRRNA report no outbreaks of intense herbivory or episodes of pathogens causing severe plant losses in the last 20 years (R. Halvorson personal communication 1995).

METHODS

In roughly the center of HRRNA, a 19.6-ha permanent grid was established by Gashwiler (1977) for use in an ecological study in 1972. Stations on the 12 × 12 grid are marked by rebar stakes and spaced 40.2 m apart. Using this grid, we randomly selected 25 stations and established 0.04-ha circular plots from the rebar-marked center points for a total sample area of 1 ha. We tallied and measured each active *P. owyheei* nest site within each plot. We placed line transects over the center of each nest site and measured the cleared disc area in north-south and east-west directions. The edge of each disc was determined by the intersection of any perennial with the N-S or E-W transect lines.

RESULTS

There were 40 active *P. owyheei* nest sites in our 1-ha sample. We found nest sites on 23 of the 25 circular plots, and the maximum number of nest sites was 3 per 0.04 ha. Mean nest density/standard error was 1.6 (±0.16) nests/0.04 ha. Characteristics of the cleared discs are shown in Table 1. Assuming a circular shape, the mean area cleared per nest site is 4.8 m^2. Factoring in the nest density results in an estimated barren area of 192 m^2/ha, or 1.92% of the total land area of the permanent grid. If the influences of *P. owyheei* are consistent throughout the 240-ha HRRNA, then ant foraging and plant cutting surrounding a total of 9600 nest sites should leave approximately 46,080 m^2 of barren land on the 240-ha site.

DISCUSSION

The premise of this article is to provide information on *P. owyheei* nest site density

TABLE 1. Characteristics of *P. owyheei* nest sites on HRRNA.

Discs	Mean (cm)	Median (cm)	Maximum (cm)	Minimum (cm)	Standard deviation (cm)	N
N-S diameter	241.1	207.5	740	60	144.4	40
E-W diameter	254.6	220.0	670	68	156.8	40

TABLE 2. *Pogonomyrmex owyheei* and *P. occidentalis* nest site densities and mean size of nest site and estimated barren area due to *P. owyheei* and *P. occidentalis* activities reported in the literature.

Source	State	*Pogonomyrmex* species	Nest site density/ha	Nest site size in m²	Estimated barren area %	Study site disturbance	Dominant vegetation
Sharp and Barr (1960)	Idaho	*owyheei*[a]	40	0.8	6.0	“misused/ depleted”	*Atriplex nuttallii / Halogeton glomeratus*
Sharp and Barr (1960)	Idaho	*owyheei*[a]	9	1.3	3.7	“vigorous stand”	*Atriplex nuttallii*
Sharp and Barr (1960)	Idaho	*owyheei*[a]	12	nr[b]	nr	not discussed	*Ariplex confertifolia*
Willard and Crowell (1965)	Oregon	*owyheei*	49–74	22.5	11–17	not discussed	*Bromus tectorum*
Wight and Nichols (1966)	Wyoming	*occidentalis*[d]	nr	65.7	nr	lightly grazed[c]	*Atriplex nuttallii*
Rogers and Lavigne (1974)	Colorado	*occidentalis*	23	1.2	0.3	ungrazed for 30 years	*Buchloe dactyloides / Bouteloua gracilis*
Rogers et al. (1972)	Colorado	*occidentalis*	28	0.7	nr	lightly grazed	*Buchloe dactyloides / Bouteloua gracilis*
Rogers et al. (1972)	Colorado	*occidentalis*	31	0.4	nr	moderate grazing	*Buchloe dactyloides / Bouteloua gracilis*
Rogers et al. (1972)	Colorado	*occidentalis*	3	0.6	0.02	heavy grazing	*Buchloe dactyloides / Bouteloua gracilis*
Clark and Comanor (1975)	Nevada	*occidentalis*	30–43	2.4–15.9	nr	varied—lightly grazed / recent burns	*Artemisia tridentata / Agropyron desertorum*
Sneva (1979)	Oregon	*owyheei*	32	9.3	3.0	grazed pasture/ no intensity specified	*Artemisia tridentata / Agropyron spicatum / Stipa thurberiana /*
Sneva (1979)	Oregon	*owyheei*	80	0.9	0.7	lightly grazed/ brush control 10 yr prior to study killed 95% of plants	*Artemisia tridentata / Agropyron spicatum / Stipa thurberiana / Bromus tectorum*
Sneva (1979)	Oregon	*owyheei*	57	1.5	0.8	lightly grazed/ brush control 22 yr prior to study killed 95% of plants	*Artemisia tridentata / Agropyron spicatum / Stipa thurberiana / Bromus tectorum*
Coffin and Lauenroth (1988)	Colorado	*occidentalis*	25	1.4	nr	moderately grazed	*Bouteloua gracilis*
Coffin and Lauenroth (1990)	Colorado	*occidentalis*	31	1.2	nr	lightly grazed	*Bouteloua gracilis*
Nowak et al. (1990)	Idaho	*owyheei*	nr	3.5	nr	no grazing or fire in 30+ yr	*Artemisia tridentata / Oryzopsis hymenoides*
Nowak et al. (1990)	Idaho	*owyheei*	nr	5.3	nr	burned 5 yr prior to sample, then ungrazed	*Artemisia tridentata / Oryzopsis hymenoides*

[a] Identified as *occidentalis*, but in the known range of *owyheei*
[b] Not reported
[c] All references to grazing refer to grazing of cattle or other livestock.
[d] *P. owyheei* was considered to be part of *P. occidentalis* until 1950.

and cleared disc size in an undisturbed area. Much of the information on areas cleared by *Pogonomyrmex* harvester ants relates to study sites with varying degrees of disturbance history. However, few studies examine the role of *P. owyheei* and *P. occidentalis* as agents of plant removal in undisturbed environments. In our study we briefly compare results of plant removal in undisturbed areas with those results presented elsewhere.

Our nest site density of 40/ha is in the approximate middle range of reported observations under a variety of land-use influences (Table 2). Disturbance may serve to increase the nest site densities at any given site up to a point. For example, Rogers and Lavigne (1974: 995) found an increase in nest site density under “light” and “moderate” grazing, but sharply reduced densities under “heavy” grazing. Findings of Sharp and Barr (1960) and Sneva (1979) also suggest increases in nest site density are associated with disturbance (Table 2). Across the range of *P. owyheei* and *P. occidentalis*, nest site densities are likely controlled by a suite of factors (soils, vegetation composition, climate, disturbance history) acting synergistically. Increases in nest site density in grazed areas probably result from alterations of the dynamics of competition between plant species that in turn modify seed density distributions

(Holldobler and Wilson 1990). On their study site in southern Arizona, for example, Davidson et al. (1984) found that harvester ant populations began to decrease approximately 2 yr after rodent populations were intentionally reduced. Davidson et al. (1984: 1780) concluded that rodent removal led to a "differential increase" in large-seeded annuals because of the cessation of granivory, and this in turn precipitated the competitive displacement of small-seeded species that were the ant's primary food source.

Although other studies have used larger sample sizes to determine nest density (e.g., Coffin and Lauenroth [1988] used a 2.5-ha sample), we believe our nest site density is a reasonable estimate for HRRNA because (1) the study site is consistent in regard to soils and vegetation, and has only minor topographic variability; (2) our standard error per sample for nest density is small, suggesting little variability within our study area; and (3) research from studies on other *Pogonomyrmex* species has shown that soil texture can affect nesting location (e.g., Johnson 1992, DeMers 1993), and that a uniform dispersion of ant colonies develops regardless of spatial scale examined (Wiernasz and Cole 1995). There appears to be little relationship between disturbance history and mean size of nest sites (Table 2). Sneva (1979) has speculated that while there may be great variability in nest site density and disc area, the potential available forage per nest site generally remains consistent, suggesting that vegetation cover and species composition can affect disc size. Soil characteristics also impact disc size, with a tendency for colonies to expand horizontally in shallow soils (Sneva 1979). Therefore, disc size may be largely linked to the amount of vegetation cover, plant species composition, and soil depth, and less influenced by disturbance than is nest density.

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FIELD MEASUREMENTS OF ALKALINITY FROM LAKES IN THE UINTA MOUNTAINS, UTAH, 1956–1991

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ABSTRACT.—Data collected from alpine lakes in the Uinta Mountains during fishery surveys by the Utah Division of Wildlife Resources indicate alkalinity has decreased in some drainages since the mid 1950s. Implications for continued monitoring, as well as environmental and recreational values, are discussed.

Key words: alkalinity, acid precipitation, alpine lakes, water quality, Utah.

Alpine lakes in the Uinta Mountains have the lowest total alkalinity of all surface waters in Utah (EPA 1982). The low alkalinity is due to the Precambrian rock geologic origin composed primarily of metamorphic quartzite, phyllite, and diamictite. Because of low alkalinity, these lakes are sensitive to acid precipitation, which may affect long-term water quality, fish, and other aquatic organisms. The Utah Division of Wildlife Resources has measured alkalinity in many of these lakes since 1956. The purpose of this paper is to document the changes in alkalinity between 1956 and 1991 in the Uinta Mountains by drainage.

METHODS

Water from lakes in the Uinta Mountains, Utah, was sampled and measured for alkalinity from 1956 to 1991 by the Utah Division of Wildlife Resources in conjunction with the fisheries surveys. Data were collected during summers on selected lakes within 16 of the 18 major drainages (Fig. 1) and during 3 designated sampling periods: mid 1950s–early 1960s (period 1), 1970s–early 1980s (period 2), and mid 1980s–early 1990s (period 3). All alkalinity data were collected in the field using colorimetric methods and converted to mg/L. In period 1, tests were made using methylpurple indicator and titrating with 0.02 N sulfuric acid. Alkalinity titrations were made at stepwise increments of 5.0 mg/L (per drop). In periods 2 and 3, tests were made with Hach (Hach Company, PO Box 389, Loveland, CO 80539) Water Ecology Kits, model AL-36B. Alkalinity titrations were made at increments of 6.8 mg/L (per drop) in all drainages, except during period 2 in Rock Creek, Duchesne, and Provo River drainages, and during period 3 in Rock Creek, Burnt Creek, and Sheep-Carter Creek drainages when the increments were 17.1 mg/L (per drop). The effects of 3 weaknesses in the available data—the lack of data sets from all drainages during all 3 periods, the 3 levels of sensitivity in the alkalinity measurements, and the differences in sample sizes—are unknown and suggest interpretive caution of the results. The significance level was set at $P < 0.05$ for the 3 comparisons of statistical testing.

To test for changes over all drainages, mean alkalinity among drainages was compared between periods using ANOVA for unequal sample sizes (Sokal and Rohlf 1981).

To test for changes in alkalinity within drainages, data were compared between periods. *T* tests of the mean were used when data from 2 periods were available, and ANOVAs for unequal sample sizes were used when 3 periods of data were available.

To test for changes in alkalinity within drainages for the same sampled lakes, I compared data between periods. *T* tests for paired comparisons were used when 2 periods of data were available, and ANOVAs for equal sample sizes when 3 periods of data were available.

RESULTS

Mean alkalinity among drainages significantly decreased ($P < 0.05$) between all 3

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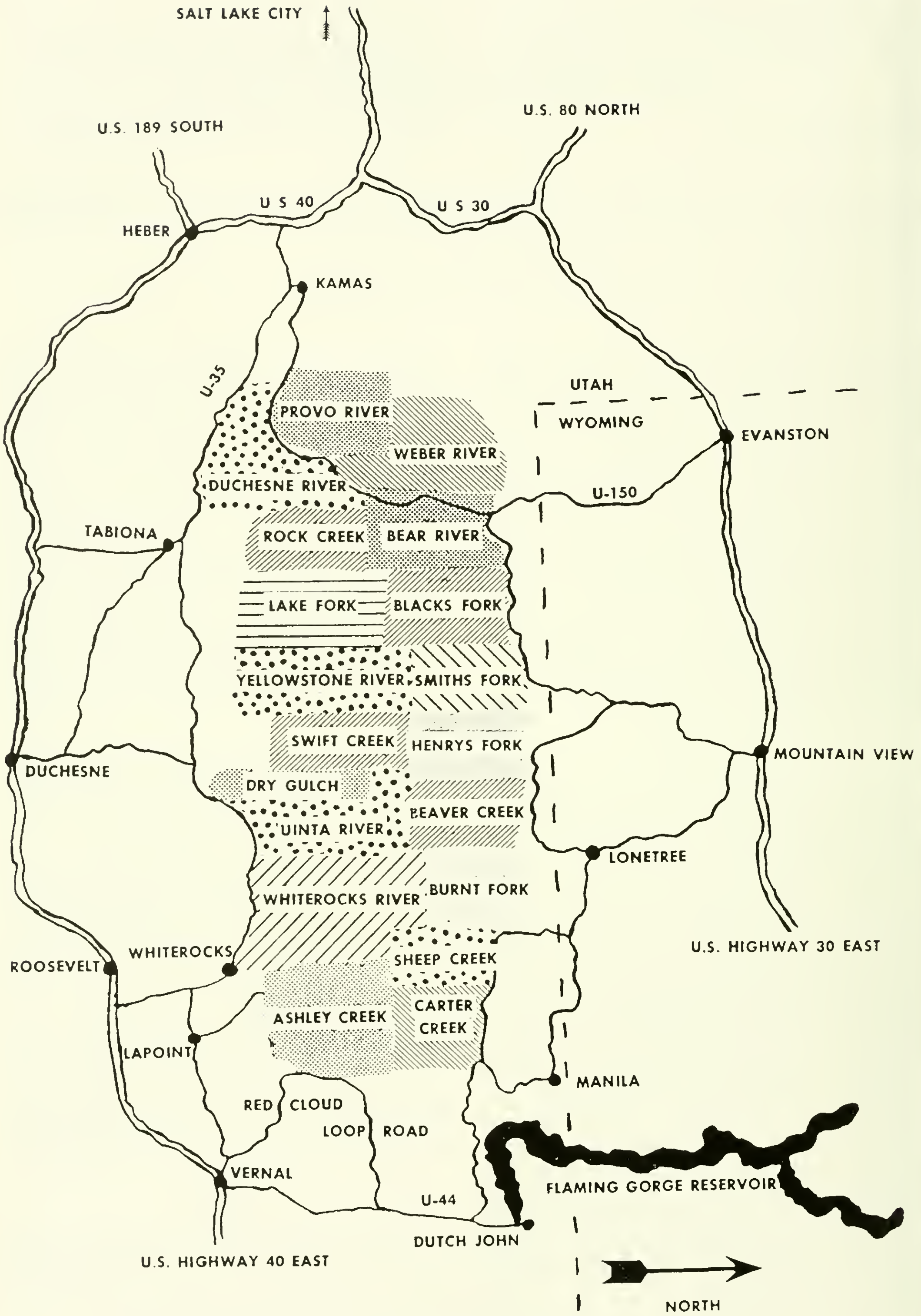
SALT LAKE CITY
U.S. 189 SOUTH
U.S. 80 NORTH
U S 40
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HEBER
KAMAS
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UTAH
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EVANSTON
PROVO RIVER
WEBER RIVER
DUCHESNE RIVER
U-150
TABIONA
ROCK CREEK
BEAR RIVER
LAKE FORK
BLACKS FORK
YELLOWSTONE RIVER
SMITHS FORK
SWIFT CREEK
HENRYS FORK
MOUNTAIN VIEW
DUCHESNE
DRY GULCH
BEAVER CREEK
UINTA RIVER
LONETREE
WHITEROCKS RIVER
BURNT FORK
U.S. HIGHWAY 30 EAST
WHITEROCKS
SHEEP CREEK
ROOSEVELT
ASHLEY CREEK
CARTER CREEK
LAPOINT
MANILA
RED CLOUD
LOOP ROAD
VERNAL
FLAMING GORGE RESERVOIR
U-44
DUTCH JOHN
U.S. HIGHWAY 40 EAST
NORTH

Fig. 1. General location and major drainages in the Uinta Mountains, Utah.

periods (Table 1) from 33 mg/L in period 1, to 23 mg/L in period 2, to 17 mg/L in period 3. (Standard deviations for all means listed in Table 1 are available from the author.)

Alkalinity within individual drainages significantly decreased in the Duchesne River and Provo River drainages between all 3 periods. Alkalinity decreased between periods 1 or 2, and period 3 in the Rock Creek, Weber River, and Whiterocks River drainages. No change in alkalinity was found between periods 1, 2, and 3 in the Bear River drainage. Similarly, no change in alkalinity between periods 2 and 3 was found from Beaver Creek, Blacks Fork, Smiths Fork, and Henrys Fork drainages. Due to lack of data, no additional comparisons could be made.

Changes in alkalinity within drainages, where data from the same lakes were available between 2 periods, were variable. Alkalinity did not change in the Rock Creek drainage between periods 1 and 3, or in the Weber River drainage between periods 1 and 2. Alkalinity also showed no change in the Rock Creek, Bear River, Blacks Fork, Smiths Fork, or Whiterocks River drainages between periods 2 and 3. However, alkalinity decreased in the Duchesne River and Provo River drainages between periods 1 and 2, 2 and 3, and 1 and 3. Alkalinity also decreased in the Weber River and Bear River drainages between periods 1 and 3, but increased in the Henrys Fork and Beaver Creek drainages between periods 2 and 3. No additional comparisons could be made.

Alkalinity in the Duchesne River and Provo River drainages where the same lakes were sampled during all 3 periods was significantly ($P < 0.05$) different between all 3 periods for both drainages. Mean alkalinity values using the combined data from these 2 drainages decreased from 37 mg/L in period 1 to 22 in period 2, to 6 in period 3. No comparisons over the 3 periods could be made from the other drainages.

DISCUSSION

Negative effects of acid precipitation on aquatic ecosystems have been well documented, particularly in Europe and eastern North America (Haines 1981a). Acid precipitation can have negative impacts on water chemistry and quality, algae, bacteria, invertebrates, amphibians, fish, waterfowl, and aquatic vegetation (Pough and Wilson 1977, EPA 1979, Haines 1981b, Kretser et al. 1983), and result in a general reduction in biodiversity (Fryer 1980).

Alkalinity and pH are directly related in maintaining aquatic ecosystems; and as alkalinity decreases, lakes become increasingly susceptible to acidification (Haines 1981a). Acidification rates were reported by Dillian et al. (1987) for 2 Canadian lakes as 2 ueq/L/yr between 1979 and 1985 with a 3-fold decrease in alkalinity accompanied by a 0.2 pH decrease.

Decreases in alkalinity have been reported in Colorado. In the Colorado Rockies, 64 lakes were compared between 1938–1960 and 1979 with a mean decrease between periods (1938–1960 vs. 1979) of 17% alkalinity (Lewis 1982). In the Mt. Zirkel Wilderness Area, Turk and Campbell (1987) reported an approximate loss of buffering capacity of <10% in most lakes they surveyed.

Data from this study indicate a 50% decrease in alkalinity since the 1950s, with the rate of decrease about 0.5 mg/L/yr in the Uinta Mountains. At this rate of decrease, studies extended for only a few years would likely show no change in alkalinity.

Contrary to our results, 2 previous studies conducted in Utah indicated no effects of acidification. In a snowmelt study of the Wasatch Mountains, Messer et al. (1982) reported a mean snowmelt pH of 6.17 and concluded that enough buffering capacity was retained in the snowpack to neutralize acid equivalents from air pollution. In a report from the Utah Technical Advisory Committee on acid deposition, Ellis (1986) concluded that although lakes and streams in the Uinta Mountains are very sensitive to acidification, no evidence was found that demonstrated acidification had occurred. The lack of acidification was based primarily on data collected in the Mirror Lake watershed during 1983–1986. Both studies suggested windblown particulates from the Great Salt Lake Desert were sufficient to buffer acid deposition.

Decreased alkalinity from alpine lakes sampled by the Utah Division of Wildlife Resources in the Uinta Mountains over 35 years indicated a slow decline in alkalinity, particularly in the Provo River and Duchesne River drainages. Unaltered, this decline may eventually result in deterioration of the aquatic ecosystem and, subsequently, recreational values.

TABLE 1. Mean total alkalinity (mg/L) by drainage from alpine lakes in the Uinta Mountains, Utah.

Combined data from all sampled lakes

Phase n = 18	Period 1			Period 2			Period 3		
Drainage	Year	n	mg/L	Year	n	mg/L	Year	n	mg/L
Rock Creek	1956	9	$31^{1,a}$	1973	3	34^{a}	1983	54	21^{b}
Duchesne River	1956	30	35^{a}	1979	7	24^{b}	1985	34	8^{c}
Provo River	1956	23	36^{a}	1979	20	23^{b}	1986	54	8^{c}
Weber River	1956	27	35^{a}	1983	3	22^{ab}	1987	16	12^{b}
Bear River	1956	5	30	1982	26	17	1989	30	21
Blacks Fork	ND[3]	—	—	1982	22	26	1989	21	25
Smiths Fork	ND	—	—	1983	24	16	1990	20	15
Henrys Fork	ND	—	—	1984	22	15	1990	21	24
Beaver Creek	ND	—	—	1984	23	20	1991	17	29
Burnt Fork	ND	—	—	ND	—	—	1984	11	17
Sheep/Carter Creeks	ND	—	—	ND	—	—	1984	32	19
Ashley Creek	ND	—	—	ND	—	—	1988	21	13
Whiterocks River	ND	—	—	1976	2	34^{a}	1985	43	14^{b}
Uinta River	ND	—	—	ND	—	—	ND	—	—
Dry Gulch	ND	—	—	ND	—	—	1987	12	14
Yellowstone River	ND	—	—	ND	—	—	1986	24	14
Lake Fork River	ND	—	—	ND	—	—	ND	—	—
Swift Creek	ND	—	—	ND	—	—	1987	17	14
Total/Mean	—	94	33^{a}	—	152	23^{b}	—	427	17^{c}

[1] Numbers with different letters across rows were significantly different, $P < 0.05$

[2] NDC = No data from common lakes available.

[3] ND = No alkalinity data collected.

Additional sampling is essential to monitor and document alkalinity and potential acidification of Uinta Mountain lakes.

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TABLE 1. Continued.

Data from the same lakes sampled during 2 periods									Data from the same lakes sampled during all 3 periods			
	1	2		1	3		2	3		1	2	3
n	mg/L	mg/L	*n*	mg/L	mg/L	*n*	mg/L	mg/L	*n*	mg/L	mg/L	mg/L
NDC[2]	—	—	8	30	24	3	34	17	NDC	—	—	—
6	35^{a}	23^{b}	21	36^{a}	5^{b}	6	23^{a}	6^{b}	6	33^{a}	23^{b}	6^{c}
14	37^{a}	21^{b}	14	38^{a}	7^{b}	15	22^{a}	5^{b}	10	41^{a}	21^{b}	6^{c}
2	33	7	8	33^{a}	10^{b}	NDC	—	—	NDC	—	—	—
NDC	—	—	5	30^{a}	13^{b}	17	20	20	NDC	—	—	—
NDC	—	—	NDC	—	—	18	24	26	NDC	—	—	—
NDC	—	—	NDC	—	—	13	11	12	NDC	—	—	—
NDC	—	—	NDC	—	—	14	12^{a}	17^{b}	NDC	—	—	—
NDC	—	—	NDC	—	—	17	22^{a}	29^{b}	NDC	—	—	—
NDC	—	—	NDC	—	—	NDC	—	—	NDC	—	—	—
NDC	—	—	NDC	—	—	NDC	—	—	NDC	—	—	—
NDC	—	—	NDC	—	—	NDC	—	—	NDC	—	—	—
NDC	—	—	NDC	—	—	2	34	14	NDC	—	—	—
NDC	—	—	NDC	—	—	NDC	—	—	NDC	—	—	—
NDC	—	—	NDC	—	—	NDC	—	—	NDC	—	—	—
NDC	—	—	NDC	—	—	NDC	—	—	NDC	—	—	—
NDC	—	—	NDC	—	—	NDC	—	—	NDC	—	—	—
NDC	—	—	NDC	—	—	NDC	—	—	NDC	—	—	—
22	35^{a}	17^{b}	56	33^{a}	12^{b}	88	23	17	16	37^{a}	22^{b}	6^{c}

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DENSITY, BIOMASS, AND DIVERSITY OF GRASSHOPPERS (ORTHOPTERA: ACRIDIDAE) IN A CALIFORNIA NATIVE GRASSLAND

Eric E. Porter[1,2], Richard A. Redak[1], and H. Elizabeth Braker[3]

ABSTRACT.—A native California perennial grassland was sampled for grasshopper populations. The grassland is managed for the preservation of the native perennial bunchgrass, *Nassella pulchra* Hitch. Grasshopper density, biomass, diversity, and richness were measured from July 1993 to October 1994. Average density of all grasshoppers was 2.30 hoppers/m^2 (0.66 *s*) for 1994 (June through August). Overall forage consumed for 1994 was 140 kg/ha, suggesting that grasshopper populations exist at economically damaging levels. Grasshoppers do not appear in the grasslands until late spring, after annual grasses have set seed. Biomass of grasshoppers peaks in July when adults are predominant. Both grasshopper density and biomass were higher in 1993 than in 1994, and a total of 5 species were found throughout the study. *Melanoplus sanguinipes* Fabricus dominated the acridid communities and accounted for more than 95% of the individuals.

Key words: Nassella pulchra, Melanoplus sanguinipes, *California native grassland, density, diversity, grasshopper herbivory, Acrididae.*

California's native perennial bunchgrass communities have been reduced to less than 1% of their original range (Heady 1977), with much of this loss attributable directly to the development of agricultural and urban areas (Huenneke 1989). Additionally, most undeveloped patches of native grasslands have converted to grasslands dominated by annual grasses native to the Mediterranean region (Jackson 1985). Factors leading to the success of these Mediterranean species are not completely understood; however, heavy grazing pressure has been implicated as a major factor that favors these more ruderal annual species (Burcham 1957). In their pristine state, before the arrival of European settlers, California's grasslands had light grazing pressure (Wagner 1989). Removal of major anthropogenic disturbances such as grazing and fire does not lead to the recovery of native perennial grasslands (White 1967, Keeley 1981). Most investigators now agree that the annual grass species should be considered naturalized, and a return to the pristine disturbance pattern will not lead to reestablishment of native grasslands (Heady 1977).

Joern (1989) suggests that through differential herbivory upon the perennial grasses (relative to annuals), grasshoppers may have contributed to the establishment of exotic annual grasses in California's native grasslands. Grasshopper herbivory is presumed to be greatest in summer months when annual grasses already have set their seed and prior to germination in the fall (Joern 1989). Therefore, only perennial grasses and summer forbs are susceptible to damage by grasshopper herbivory. Furthermore, many grasshopper species exhibit preference for perennial grasses in the field (Capinera and Sechrist 1982). Joern (1989) suggests that this phenology-based, selective damage could reduce the competitive ability of native perennial grasses against naturalized annuals.

There are few data available to support or refute Joern's (1989) hypothesis beyond basic surveys of grasshoppers throughout the state (Strohecker et al. 1968). No population or community-level studies are available for California's grasshoppers in California native perennial grasslands (e.g., population density, species abundance, and biomass estimations). The objective of this study was to describe the grasshopper community found in a representative remnant stand of native perennial grassland over a period of 2 seasons. These data will provide information necessary to understand the role of grasshoppers in California's grasslands and should lead to more informed decisions for grassland conservation managers.

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METHODS AND MATERIALS

Study Area

The study was conducted in the Santa Rosa Plateau Ecological Reserve (SRPER), located 10 km west of Murrieta, California. The site is actively managed by The Nature Conservancy for the restoration and preservation of its rare habitats. The reserve covers 2800 ha and contains about 1200 ha of native perennial grasslands amongst oak woodlands, coastal sage scrub, and chaparral. Six sites were established within the perennial grasslands. These sites were burned in June of 1992 as a management practice to retard annual grass establishment. Grazing has been excluded from all sites since at least 1990 (R. Wells, SRPER reserve manager, personal communication).

Purple needle grass (*Nassella pulchra* A. Hitch.) is the most abundant native grass in the reserve. Common exotic annual grasses include slender wild oats (*Avena barbata* Link) and red brome (*Bromus laevipes rubens* Labill). Common forbs include annual bursage (*Ambrosia acanthicarpa* Hook.), doveweed (*Eremocarpus setigerus* H.), and filaree (*Erodium cicutarium* L'Hér.; Lathrop and Thorne 1985).

Grasshopper Sampling

Six transects were arbitrarily placed throughout the perennial grassland areas representing maximum topographic and vegetational heterogeneity. Each transect measured 200 m long by 20 m wide. Grasshopper density was determined with twenty 0.25-m^2 hoops (Onsager and Henry 1977, Thompson 1987). Hoops were placed along each transect at 10-m intervals. Density was determined monthly beginning in July 1993. Grasshopper days (GHD) and forage consumption estimates were determined following Onsager (1984). GHD is a measure of total grasshoppers found per m^2 for a given year. Forage consumption is an estimate of the yearly forage consumption of grasshoppers based on estimated daily consumption (0.65 times body weight) and GHD. Biomass-days were calculated using the same formula for GHD replacing grasshoppers/m^2 with g/m^2. When possible (density >0.5 grasshoppers/m^2), 100 individual grasshoppers were collected from each site and frozen immediately. These collections were taken directly following density counts and were made in August and October 1993; June, July, and August 1994. Grasshoppers were identified to species and weighed to the nearest mg. Identifications provided the proportion of adults (p_a) in each sample. Given total density (d), adult density (d_a) was calculated with the following formula:

$$d_a = (d) * (p_a).$$

Species diversity was measured using the Shannon-Weiner index (Pielou 1977). Feeding category designations follow Capinera and Sechrist (1982) and Otte (1981; graminivorous, forbivorous, or mixed). Identification of nymphal stages is difficult, and damaging feeding does not occur until the 4th instar (Onsager 1984). Therefore, where possible, adult grasshopper data are analyzed separately from total grasshopper data.

RESULTS

Species of grasshoppers collected are listed with subfamily and known feeding preferences (Table 1). Average grasshopper density for the 1994 season (June–August) was 2.30 grasshoppers/m^2 (Table 1). Density measurement began too late in the season to estimate an average for 1993. A total 198 GHD were determined for 1994, leading to an estimated 140 kg/ha of forage consumed. Density estimates of zero grasshoppers/m^2 were found from November 1993 through May 1994. Density peaked in June for 1994 at 2.9 grasshoppers/m^2. This peak in density was dominated by immature stages (Fig. 1A). Density measures were higher in 1993 than in 1994 for all paired sample dates in July, August, and October ($f = 4.69$, df = 1, 20; $P = 0.041$). Biomass peaked in July when most grasshoppers were in the adult stage (Fig. 1B). Biomass days for 1994 totaled 13.2 g-d/m^2 (Table 1). Peak biomass (August) was higher in 1993 than in 1994 ($t = 2.43$; $P = 0.036$).

The Shannon-Weiner diversity index, including adults and nymphs combined, averaged 0.140 over the 5 collection dates (Fig. 2A). The peak in adult diversity, in June 1994, represents only 6 individuals of 2 species. Combined adult and nymph species richness averaged 3.4 for the sampled dates. Highest species richness was found in August. In total, 5 grasshopper species were found in these sites for the collection dates.

TABLE 1. Species of grasshoppers collected in 1993–94 on the SRPER with known feeding types (Capinera and Sechrist 1982, Otte 1981) and appearance, % composition, GHD, biomass-days, average density, and weight as calculated for the sampling period.

Species	Subfamily[a]	Feeding type[b]	Appearance	% composition	GHD[c] (grasshopper days/m²)	Biomass-days[c]	Average density (#/m²)[c]	Average adult weight (mg)
Cannula pellucida Scudder	O	G	May–Aug	0.2	0.36	0.076	<0.01	72
Melanoplus aridus Scudder	M	N/A	Jun–Aug	0.3	0.50	0.031	<0.01	90
Melanoplus sanguinipes Fabricus	M	M	May–Oct	97.5	193.47	12.754	2.24	132
Mermeria bivittata Serville	G	G	May–Oct	1.6	3.18	0.375	0.03	81
Psolessa texana Scudder	G	G	Jun–Oct	0.5	0.89	0.121	0.01	61
TOTAL					198	13.240	2.30	131

[a] O = Oedipodinae, M = Melanoplinae, G = Gomphocerinae
[b] G = grass, M = mixed, N/A = not available
[c] GHD, biomass-days, and average density for 1994 season only

DISCUSSION

Grasshopper populations in the SRPER appear in late May or early June. Grasshopper biomass peaks, and the most severe herbivory occurs, in July and August. By this time, annual grasses have already died and their seeds are buried and protected from aboveground herbivory (Savelle and Heady 1970). Grasshopper densities decrease dramatically after August, and few are present by October. Annual grasses are triggered to germinate after the first fall rains (Heady 1958). By the time these rains arrive, grasshopper densities are near 0; therefore, both the mature annual grasses and their seedlings escape serious grasshopper herbivory.

One species, *Melanoplus sanguinipes*, accounted for over 95% of grasshoppers found in SRPER (Table 1). This species commonly damages crops and rangelands throughout North America (Hewitt 1977). Intense outbreaks are common and can remove up to 92% of aboveground vegetation (Nerney 1966, Hilbert and Logan 1981). *Melanoplus sanguinipes* is classified as a mixed feeder and may prefer grasses or forbs depending upon the area sampled. If *M. sanguinipes* feeds extensively on grasses within the SRPER, given its phenology, it will damage perennial grasses more than annual grasses. Overall forage consumption was 140 kg/ha in 1994, which is an economically damaging level according to Onsager (1984). However, using *M. sanguinipes* in a shortgrass prairie community, Quinn et al. (1993) found significant reductions in grass biomass only at grasshopper densities equivalent to 845 GHD or greater. We found only 198 GHD in 1994, suggesting that densities during these years may not greatly affect grassland plant community dynamics according to Quinn (1993).

The climate of California's grasslands makes comparison with other North American studies difficult. Most comparable studies examine tallgrass, mixed-grass, and shortgrass prairies east of the Sierra Nevada. The dry, hot summers that characterize California's Mediterranean climate severely limit growth (Risser et al. 1981). Regrowth following summer herbivory is similarly limited. Clearly, only perennial grasses are susceptible to herbivory at this time, and the actual effect of such herbivory in California grasslands is undocumented. Therefore, specific studies on the effect of grasshopper herbivory on native California grasslands must be conducted to predict the level and type of infestation, if any, that may favor annual grasses over native perennial species.

California's grasshopper fauna is rich, compared to other North American regions, with over 120 species (Joern 1989). About half of these grasshopper species are considered rangeland species. Southern California has the richest grasshopper fauna of any region in California (Strohecker 1968). Still, richness for the SRPER was very low compared to other studies of North American grasslands. Few studies report diversity indexes, but richness has been measured for other native North American grasslands. Richness is nearly always

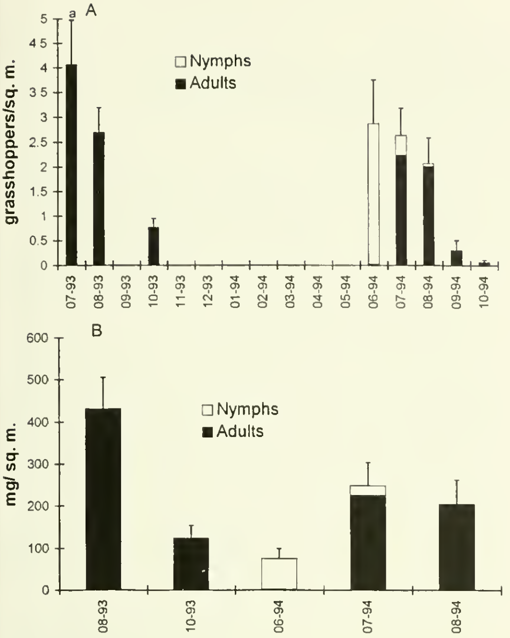

Fig. 1. (A) Grasshopper density for all sampling dates and (B) biomass for dates collected (a = proportion of adults vs. nymphs unknown for July 1993).

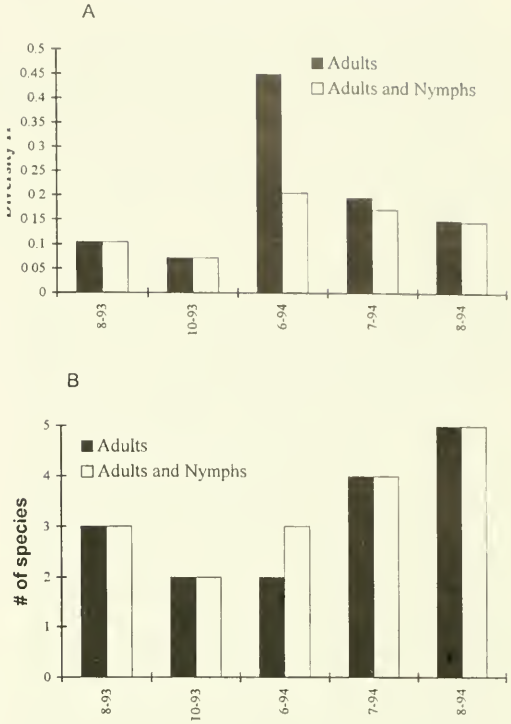

Fig. 2. Diversity (A) and species richness (B) for all dates in which collections were made.

higher than the value of 5 species determined here (e.g., Joern 1982, Evans 1988). We feel it is likely that the grasshopper community is particularly species depauperate due to isolation of the SRPER grasslands (MacArthur and Wilson 1967). Frequent burning of the grasslands may also help explain the low diversity found in the SRPER. On the other hand, burned sites contain more even species compositions than unburned grasslands and contain species not found in unburned sites (Porter 1995). Therefore, we feel that to preserve the diversity of not only grasshoppers but presumably many arthropods, birds, plants, and other taxa, it may be necessary to preserve larger tracts of native grasslands. Furthermore, the effects of grasshopper herbivory in these grasslands must be accounted for in a well-rounded conservation effort.

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SUMMER NOCTURNAL ROOST SITES OF BLUE GROUSE IN NORTHEASTERN OREGON

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Key words: Blue Grouse, Dendragapus obscurus, *nocturnal, Oregon, roost.*

Avian habitat studies frequently focus on diurnal habitat use because of ease of observation and high levels of activity associated with breeding and foraging. Nocturnal habitat use may be critical for all birds but has received far less attention. Thus, there is a need to better understand nocturnal habitat use, especially by crepuscular and diurnal birds, and factors that may contribute to this use.

Blue Grouse (*Dendragapus obscurus*) are associated primarily with true fir (*Abies* spp.) and Douglas-fir (*Pseudotsuga menziesii*) forests in mountainous regions of western North America (Johnsgard 1983). Breeding season habitat associations often include nonforested and shrub or steppe regions. These birds are diurnal with increased activity in the morning and evening hours. Pekins et al. (1991) determined that both diurnal and nocturnal winter roosts of Blue Grouse were located in conifers. Blue Grouse shifted from eating conifer needles in winter to ground-layer vegetation in summer and fall in northeastern Oregon (Crawford et al. 1986). Blue Grouse summer habitat studies have dealt with diurnal activities (Mussehl 1963, Bendell and Elliot 1966, Zwickel 1975), but nocturnal observations are minimal. Johnson (1929) witnessed a brood fly into a tree, apparently to roost overnight, and Blackford (1958, 1963) observed ≥ 3 adult males flying into "roost trees" in spring, where they presumably stayed overnight. Blackford (1963) also observed a male displaying on the ground approximately 1 h after dark. Zwickel (1992) suggested that ground roosting may occur, particularly on breeding ranges where trees are unavailable or before chicks are able to fly. In the course of monitoring radio-equipped Blue Grouse during summer, we identified 20 independent nocturnal roost sites. Our objective here is to describe these roost sites.

STUDY AREA AND METHODS

The study area is located in northeastern Oregon, 30 km north of Enterprise in the Wallowa-Whitman National Forest in Wallowa County. Elevation ranges from 900 to 1500 m, with ridge slopes as great as 35°. North-facing slopes are dominated by stands of Douglas-fir and ponderosa pine (*Pinus ponderosa*), and common shrubs are mallow ninebark (*Physocarpus malvaceus*), snowberry (*Symphoricarpos albus*), and big huckleberry (*Vaccinium membranaceum*). Bunchgrass meadows, predominantly bluebunch wheatgrass (*Agropyron spicatum*) and Idaho fescue (*Festuca idahoensis*), occur on south-facing slopes. Cattle graze parts of the area during summer months, resulting in variable grass cover.

Grouse were captured in walk-in traps and fitted with poncho- or necklace-mounted radio transmitters, 15 to 18 g (Advanced Telemetry Systems, Inc., Isanti, MN, and Telemetry Systems, Inc., Mequon, WI), from June through August 1993. Radio-equipped juvenile birds were ≥ 500 g, capable of flight, and ≥ 1 mon of age. Each radio-equipped bird was located at night once between 5 July and 3 August 1993. In addition to radio telemetry, a spotlight was used to verify the location of the bird. The exact roost site was identified by the presence of fresh fecal droppings. When 2 or more grouse were observed roosting together (< 10 m apart) only 1 roost site was counted for use in analyses to ensure independence of locations.

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RESULTS AND DISCUSSION

Twenty-five radio-equipped Blue Grouse and 38 birds without radios were located at 20 independent nocturnal roost sites (Table 1). The radio-equipped birds consisted of 12 adults and 13 juveniles; sexes and ages of the other birds were unknown. All roost sites were on the ground. Males usually roosted alone, whereas hens and juveniles frequently roosted together. Sixteen of 20 independent roosts, including birds of all sex and age groups, were in grass of a relatively consistent height; the others were in forbs ($n = 2$) and shrubs ($n = 2$). Twenty-three of 25 radio-equipped birds were within 50 m of potentially useful roost trees. An adult female and a juvenile female roosted 75 and 100 m from trees, respectively, both easy flight distances for grouse. Adult males usually roosted closer to trees than other birds.

During daytime, radio-equipped birds were seldom located in trees (<1% of 614 observations, July–August 1991 through 1993; E. Pelren unpublished data). However, almost all birds flushed during the day landed in trees, and conifer needles were found in crops of birds taken from the study area in August and September 1981 and 1982 (Crawford et al. 1986). Crawford et al. also found plants such as prickly lettuce (*Lactuca serriola*), yellow salsify (*Tragopogon dubius*), wild buckwheat (*Eriogonum* spp.), and snowberry (*Symphoricarpos albus*), as well as short-horned grasshoppers (*Acrididae*) in at least 30% of 145 Blue Grouse crops in this area. Douglas-fir needles were found in only 16% of the crops. This greater use of ground-cover forage and invertebrates corresponded with observed diurnal and nocturnal use of ground habitat by Blue Grouse in summer. Blackford (1963) suggested that selection of roosting sites may result from foliage preference and feeding habits. Motion sensors on grouse transmitters indicated that some birds continued foraging on moonlit nights, which implied that benefits of feeding outweighed energy loss associated with movement or increased risk of predation.

Pekins et al. (1991) suggested Blue Grouse selection of conifers as roosts in winter may be based primarily on thermal properties of the sites. Higher temperatures during summer make thermal considerations less relevant to survival than during winter. The lowest temperature we noted at a nocturnal roost site was 4°C, well above the lower critical temperature of −10°C to −15°C (Pekins 1988).

Hines (1986) found that 96% of juvenile and adult Blue Grouse mortalities were the result of predation. In winter, Blue Grouse in trees may be less conspicuous or available to predators than those on the ground (Bergerud and Gratson 1988), and Pekins (1988) observed snow roosting only occasionally, after heavy snowstorms. However, lack of snow and increased presence of grasses, forbs, and shrubs in summer, along with cryptic coloration of Blue Grouse, provide ground-layer camouflage superior to that available in winter. Food availability may outweigh any increased risk of predation and account for use of nocturnal ground roosts by Blue Grouse in summer where selection of ground roosts occurs.

TABLE 1. Characteristics of 20 Blue Grouse nocturnal roost sites, northeastern Oregon, July–August 1993.

	Adult male	Adult female	Juvenile male	Juvenile female
No. of roost sites	6	6	3(8[a])	5
No. of other birds	1	16[b]	7	9[c]
Plant cover at roost				
Grass	4	6	3(8[a])	3
Forb	1	0	0	1
Shrub	1	0	0	1
Plant height (m) at roost				
Median	0.50	0.45	0.50[a]	0.75
Range	0.25–1.20	0.25–1.00	0.30–0.75[a]	0.30–1.30
Distance (m) to potential roost tree				
Median	4.5	37.5	50.0[a]	20.0
Range	1.0–40.0	15.0–75.0	3.0–75.0[a]	5.0–100.0

[a] Includes data for 5 radio-equipped juvenile males that were with radio-equipped adult or juvenile females.

[b] Does not include 2 radio-equipped juvenile males that were with radio-equipped adult females.

[c] Does not include 3 radio-equipped juvenile males that were with radio-equipped juvenile females.

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OOCHORISTICA SCELOPORI (CESTODA: LINSTOWIIDAE) IN A GRASSLAND POPULATION OF THE BUNCH GRASS LIZARD, *SCELOPORUS SCALARIS* (PHRYNOSOMATIDAE), FROM ARIZONA

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Hobart M. Smith[4], and Quynh A. Truong[1]

Key words: Sceloporus scalaris, *bunch grass lizard, Phrynosomatidae,* Oochoristica scelopori, *Cestoda, Arizona.*

The bunch grass lizard (*Sceloporus scalaris* Wiegmann, 1828) is known from the Huachuca, Dragoon, Santa Rita, and Chiricahua mountains of Arizona, the Animas Mountains of New Mexico, and in the Sierra Madre Occidental and Sierra del Nido of Mexico, usually above 1830 m, but a few isolated valley populations occur as low as 1200 m (Stebbins 1985). To our knowledge, the only report of helminths of this species was a study of a high-elevation (2438–2560 m) Chiricahua Mountain population of *Sceloporus scalaris slevini* by Goldberg and Bursey (1992a). The purpose of our note is to report on a helminthological examination of a low-elevation (ca 1524 m) grassland population of *S. scalaris slevini* Smith, 1937 from Arizona, and to compare our findings with those of Goldberg and Bursey (1992a).

We examined 51 *S. scalaris slevini* (mean snout-vent length 51 ± 3.4 mm [*s*], range 40–55 mm) collected (mostly by hand, a few by dust shot) on the Sonoita Plain, elevation ca 1524 m (31°39′N, 111°32′W), in the vicinity of Elgin, Santa Cruz County, Arizona. Specimens were deposited in the University of Colorado, Museum of Natural History, Boulder, Colorado as UCM 57259-57282; 57284-57286; 57289-57292; 57295-57298; 57300-57305; 57307-57310; 57313-57316; 57318-57319. UCM 57318-57319 were collected 20 August 1989; others were collected 12–19 July 1990.

The abdomen was opened, and the esophagus, stomach, and small and large intestines were removed from the carcass. Each organ was slit longitudinally and examined under a dissecting microscope. The liver and body cavity were also examined. Each helminth was identified using a glycerol wet mount. Representative cestodes were stained with hematoxylin and mounted in balsam for further examination. Voucher specimens were deposited in the U.S. National Parasite Collection, Beltsville, Maryland 20705 (USNPC 85053). Terminology use is in accordance with Margolis et al. (1982).

Only 1 helminth was found, the cestode *Oochoristica scelopori* Voge and Fox 1950. Prevalence of infection was 10% (5 of 51); mean intensity = 1.2 ± 0.45 [*s*], range 1–2.

In the only other investigation of helminths of *S. scalaris*, Goldberg and Bursey (1992a) reported finding tetrathyridia of the cestode *Mesocestoides* sp. (prevalence 8%) and larvae of the nematode *Physaloptera* sp. (prevalence 3%). That study was done on a coniferous forest high-elevation population (approximately 2500 m) in the Chiricahua Mountains, whereas the current study considered a low-elevation population (ca 1524 m) on the Sonoita Plain, located ca 126 km SE of the Chiricahua Mountains study site. Although both populations harbored mutually exclusive helminth faunas, additional work on larger *S. scalaris* samples from these sites will be required to determine the constancy of these differences.

Oochoristica scelopori is a common cestode of North American lizards and has been found in 14 other North American phrynosomatid lizards (Table 1). In addition, Amrein (1951) and Telford (1964) reported finding *O. scelopori* in the xantusiids, *Xantusia henshawi*, *X. riversiana*, and *X. vigilis*. Measurements of various structures of these cestodes were strikingly different from the measurements as given

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TABLE 1. Definitive hosts of *Oochoristica scelopori* in North America.

Host	Locality	Prevalence	Reference
Crotaphytus collaris	California	100% (1/1)	Telford 1970
Gambelia wislizenii	California	40% (2/5)	Telford 1970
Sceloporus clarkii	Arizona	5% (1/20)	Goldberg et al. 1994
S. graciosus	California	not given	Voge and Fox 1950
	California	10% (7/71)	Telford 1970
	Idaho	22% (2/9)	Waitz 1961
	Idaho	1% (1/118)	Lyon 1986
	Utah	5% (1/22)	Pearce and Tanner 1973
S. jarrovii	Arizona	10% (47/489)	Goldberg and Bursey 1990
	Arizona	3% (1/31)	Goldberg and Bursey 1992b
	Arizona	5% (15/302)	Goldberg et al. 1995a
S. magister	Arizona	(?/3)	Walker and Mathias 1973
	Texas	6% (1/17)	Goldberg et al. 1995b
S. occidentalis	California	20% (13/65)	Voge and Fox 1950
	California	23% (27/116)	Telford 1970
	Idaho	11% (2/19)	Lyon 1986
	Oregon	33% (20/60)	White and Knapp 1979
	Utah	9% (1/11)	Pearce and Tanner 1973
S. olivaceus	Texas	3% (2/61)	Goldberg et al. 1995b
S. orcutti	California	22% (16/74)	Goldberg and Bursey 1991
S. poinsettii	Texas	30% (3/10)	Goldberg et al. 1993
S. scalaris	Arizona	10% (5/51)	this paper
S. undulatus	Arizona	6% (3/48)	Goldberg et al. 1994
Uma inornata	California	7% (1/15)	Telford 1970
U. notata	California	42% (10/24)	Telford 1970
Urosaurus graciosus	California	6% (2/34)	Telford 1970

in the original description of *O. scelopori* by Voge and Fox (1950). Amrein (1951) reported the average length of 25 mature cestodes from *X. henshawi* and *X. vigilis* to be 15.82 mm; the cestodes from *X. riversiana* measured 33–37 mm. Telford (1964) indicated his cestode specimens from xantusiid lizards were less than 45 mm. Both Amrein and Telford identified these cestodes as *O. scelopori.* Bursey and Goldberg (1992) found Amrein's measurements of cestodes from *X. henshawi* and *X. vigilis* to approximate the measurements of *O. bezyi,* whereas Telford's measurements of cestodes from *X. riversiana* approximated measurements of *O. islandensis* and suggested that *X. henshawi, X. riversiana, and X. vigilis* be removed from the host list of *O. scelopori,* leaving only phrynosomatid lizards as hosts for *O. scelopori.*

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POCKET GOPHERS DAMAGE SALTCEDAR (*TAMARIX RAMOSISSIMA*) ROOTS

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Key words: saltcedar, Tamarix ramosissima, *pocket gopher,* Thomomys bottae, *tamarisk, Owens Valley, invasive plant, exotic plant.*

Saltcedar (*Tamarix ramosissima* Ledeb., Tamaricaceae) is an invasive, exotic woody shrub native to Asia (Baum 1978, Hickman 1993) that has colonized extensive areas throughout the western United States (Robinson 1965, Brotherson and Winkel 1986). Saltcedar possesses many characteristics that render it a nuisance plant (Brotherson and Winkel 1986), and because it has been viewed as a threat to native vegetation communities, researchers have examined its ecology (Carman and Brotherson 1982, Brotherson and Winkel 1986, Shafroth et al. 1995), water consumption (Robinson 1958, van Hylckama 1970, Davenport et al. 1982, Bureau of Reclamation 1992), and cost of control efforts (Brotherson and Field 1987, Neill 1990, Barrows 1993). It is known to inhibit flows in creeks and springs (Robinson 1965, Rowlands 1990); thus, its spread has been detrimental not only to native vegetation but also to native wetland and aquatic fauna (Neill 1983).

Although efforts are under way in the United States to develop biocontrol agents using insects that occur on saltcedar in its native range (DeLoach 1990), to date there have been no reports of native herbivores, insects, or diseases causing saltcedar mortality. Herein we report the first known mortality caused by native mammals on saltcedar.

Our discovery occurred in Owens Valley, California. Water has been exported from Owens Valley—located in the rain shadow created by the Sierra Nevada range directly to its west—since 1913. Alteration of natural water flows created conditions favorable to the spread of saltcedar (Cashore 1985, Babb 1987).

During the winter of 1995, when foliage was absent from saltcedar, we observed that a few plants within a young, even-aged stand were dead. Some of the plants were leaning over, supported by neighboring plants. Upon inspection, we observed that dead plant taproots had been gnawed apart approximately 10 cm beneath the soil surface. Teeth marks were clearly visible on the tapered stumps. In addition, prolific gopher tunneling was evident within and around the saltcedar stand, and excavated dirt mounds were located near the dead saltcedar. Examination of growth rings of plants within the stand showed the saltcedar plants to be 7 years old in 1995.

In early April 1995, when saltcedar was just beginning to break bud, we revisited the site to quantify the extent of animal damage and to capture and identify the species tunneling at the site. We examined plants by working from one end of the stand toward the center. Every saltcedar plant in approximately 1/2 of the stand was sampled, for a total of 545 plants. Height was measured, and then plants were tugged to detect the degree of below-ground damage. If tugged plants freely exited the soil and had no attached live roots, the damage was scored as fatal. All of these plants appeared dead, no resprouting was evident, and each had a chewed taproot stump, the diameter of which was measured and recorded. If tugged plants could be pulled from the ground easily, but still had live laterals above the chewed taproot, they were noted as sustaining severe damage. In these instances, diameter of the largest chewed root was measured. Typically, these plants had many dead, but a few living, branches. If tugged plants felt loose, but could

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not be easily pulled from the soil, they were scored as sustaining minimum damage. If tugged plants were tightly rooted in the soil, we assumed no root damage. The majority of branches on plants in both these categories appeared alive.

Results of gopher damage are listed in Table 1. Nearly 23% of the plants sampled had experienced some degree of gopher damage; of these, 7.0% were dead as a result of gophers, 5.3% had been severely affected, and 10.6% had been minimally affected. The diameter of gopher-chewed roots ranged from 11 mm to 55 mm and averaged 27.7 mm.

Gopher damage appeared to affect plant height; analysis of variance revealed significant height differences between plants in the 4 categories of damage (F = 4.463, *P* = 0.004, df = 3). However, saltcedar plants not damaged by gophers tended to be only slightly taller than plants sustaining gopher damage (Table 1), suggesting that gopher damage had been relatively recent.

The study area was searched for evidence of active gopher mounds. Early in the evening, 7 active mounds were excavated, and Sherman live-traps baited with seeds and fresh plant material were placed at the tunnel level. These traps were then covered with soil, using local materials to prevent cave-ins at the trap entrance. Trapping was done under the provision of a scientific collector's permit issued by the California Department of Fish and Game. Traps were checked the following morning shortly after sunrise.

From the 7 traps set in active gopher tunnels, 1 valley pocket gopher (*Thomomys bottae*) (Ingles 1965) was captured. Two other traps were found packed with soil, presumably by gophers. The 4 remaining traps showed no obvious sign of gopher activity.

These data are the first reported evidence of a native species, *Thomomys bottae*, inducing mortality in the exotic *Tamarix ramosissima*.

The proximity of a saltcedar stand to gopher habitat may increase its susceptibility to gopher damage. At our site, gopher mounds appeared more extensive in the alkali meadow immediately adjacent to the saltcedar stand than in the stand itself. We subsequently made observations at other even-aged stands of saltcedar that occur adjacent to alkali meadows at other locations in Owens Valley and in Deep Springs Valley. Again we found gopher damage, so the phenomenon is not isolated to this single stand.

TABLE 1. Extent of gopher damage within a stand of saltcedar plants in the Owens Valley.

Gopher damage	# plants	% of total	Avg. ht. (cm)	$\pm s$
None	420	77.0	128.9	33.3
Minimum	58	10.6	120.3	30.5
Severe	29	5.3	116.2	32.6
Fatal	38	7.0	113.4	25.3
All total	545	100.0	126.2	32.8

In general, the influence of fossorial animals on plant communities has received relatively little research attention (Andersen 1987). Although gophers may kill or slow the growth of saltcedar, their long-term effects on stand size and vigor or on saltcedar establishment in the meadow remain unknown. Other researchers have found that pocket gophers cause significant woody plant mortality in a variety of plant communities (Crouch 1971, Marsh and Steele 1992, Cox and Hunt 1994, Ferguson and Adams 1994), and Huntly and Inouye (1988) and Cantor and Whitman (1989) reported that tree encroachment into meadows was significantly slowed when gophers were present in meadows. However, given the vigorous growth of saltcedar in general, gopher damage may merely thin the stand, allowing the remaining individuals to continue unabated.

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SALTCEDAR (*TAMARIX RAMOSISSIMA*), AN UNCOMMON HOST FOR DESERT MISTLETOE (*PHORADENDRON CALIFORNICUM*)

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Key words: Phoradendron californicum, Tamarix ramosissima, *mistletoe, saltcedar, host, parasite.*

The genus *Tamarix* (saltcedar) contains approximately 54 species of phreatophytic plants whose origins are in Europe, Asia, and Africa. Several members of the genus were introduced into the United States in the early 1800s, mainly as ornamental plants. Approximately 8 species have since escaped cultivation and have become naturalized to varying degrees (Baum 1967). *Tamarix ramosissima* Ledeb. has become established in riparian areas throughout the West and Southwest, where it has proven to be an aggressive invader that eventually displaces native vegetation.

Desert mistletoe (*Phoradendron californicum* Nutt.) is a native parasitic plant that grows on several species of riparian plant hosts. Its range includes southern Nevada, southwestern Utah, southeastern California, southwestern Arizona, and northern Baja California, Sonora, and Sinaloa (Benson and Darrow 1981). Previously published information on hosts for desert mistletoe include Blumer (1910), Shreve and Wiggins (1964), Walters (1976), Daniel and Butterwick (1992), and Overton (1992), none of whom mentions *T. ramosissima.* Holland et al. (1977) and Benson and Darrow (1981) state that "saltcedar" and "the introduced tamarisks" are possible hosts, while Munz and Keck (1965) and McDougall (1973) list *Tamarix* but mention no particular species. Cohan et al. (1978) state that *P. californicum* does not occur in saltcedar. This paper describes 2 occurrences of *P. californicum* on *T. ramosissima* in southern Nevada.

I found the 1st parasite and host specimen on 27 June 1995 at Hiko Springs in Clark County, Nevada, approximately 11 km west of Laughlin along State Highway 163 (3,894,000 N 711,650 E) at an elevation of 605 m (Fig. 1). A 2nd specimen was found on this host tree on 16 October 1995. Voucher specimens from 1 parasite and host are deposited in the Department of Biological Sciences herbarium, University of Nevada, Las Vegas, accession number 38971.

The host tree was growing in a canyon approximately 2 m from a small, flowing stream on quartz monzonite-derived soil. The first mistletoe clump measured 33 cm long × 32 cm high × 14 cm wide and was growing on the southwest side of a branch 2.1 m above the ground. The branch to which the mistletoe was attached measured 5.2 cm in diameter and 16.2 cm in circumference. The length of the branch from trunk to point of mistletoe attachment was 2.1 m. The trunk base of the 5-m-high saltcedar measured 8 cm in diameter and 29 cm in circumference, which would indicate an age of approximately 24 yr (based on average value of California and Arizona sites as reported by Smith 1989). The 2nd mistletoe also faced southwest and was located on the main trunk of the tree .9 m above the ground. It was a newly sprouted plant that consisted of only 12 stems, the longest of which measured 4 cm. Both mistletoes and the host tree appeared to be healthy, actively growing specimens. The parasites were young plants and were a more vivid green than other mistletoes in the area. Sex of the mistletoes could not be determined.

Other hosts for *P. californicum* at this site include catclaw acacia (*Acacia greggii*), honey mesquite (*Prosopis glandulosa*), and creosote bush (*Larrea tridentata*). Although many other *Tamarix* trees occur here, none have been infected by mistletoe. Desert mistletoe is usually spread from host to host by birds, which ingest the seeds and later defecate them onto a branch. Two bird species that occur frequently at this

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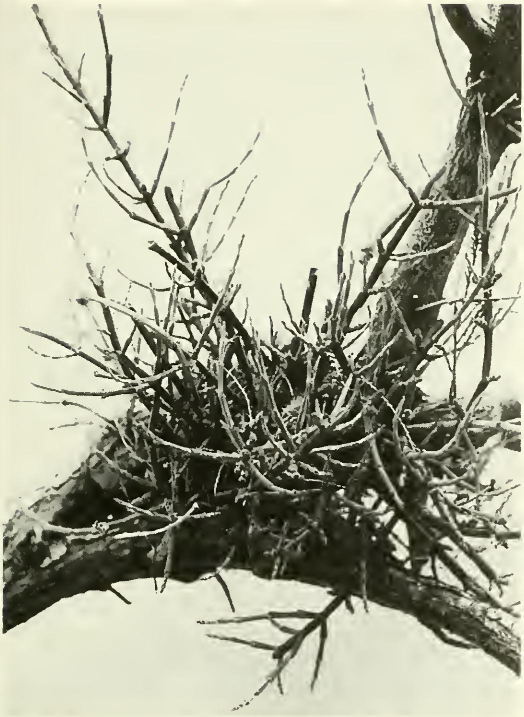

Fig. 1. Parasite *Phoradendron californicum* growing on host plant *Tamarix ramosissima.*

site and have been seen feeding on mistletoe and perching in saltcedar are the Phainopepla (*Phainopepla nitens*) and Northern Mockingbird (*Mimus polyglottos*) (personal observation).

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BOOK REVIEW

Wild Plants of the Pueblo Province. Exploring Ancient and Enduring Uses. William W. Dunmire and Gail D. Tierney. Foreword by Gary Paul Nabhan. Museum of New Mexico Press, Santa Fe, NM. 1995. 290 pp. $19.95, softback.

This book immediately appears field worthy and feels good in the hands. And that's simply judging the book by its cover! Once opened there is much to praise about this text. The authors have succeeded in putting together a wonderfully interesting and well-written field guide for the lay person as well as a useful reference for serious students and professionals interested in ethnobotany of the Southwest. Within 9 chapters of text, an illustrated section involving about 73 plants, and an extensive chart summarizing plant uses, the reader learns of the ecology, representative flora, ethnobotany, and cultural history of the Pueblo Province. The original intent of the book was to provide a guide to commonly seen plants of Bandelier National Monument and the Pajarito Plateau in central New Mexico, and a discussion of the plants' prehistoric and recent uses. The authors have surpassed this goal.

The 9 chapters reveal a cohesive and interesting history of the people, plants, and land itself. Ample information provides the reader insight as to how these elements interact and what the consequences of those interactions have been and continue to be. It is easy not only to move through the spatial and geographical regions, but to enjoy a voyage in time as well and feel as if you were there. Line drawings, photographs, and maps lend additional interest to the text. Although there is a great deal of information given about vegetative zones, human history, and other topics, the authors have retained the importance of plants by referencing particular species wherever appropriate. The chapter on indicator species is particularly interesting and useful. This is a subject that few field guides address, and yet it is so easily applied and can be observed in the field when adequate information is provided. The main focus of the text is the center section that includes photographs and descriptions of 73 plants. Line drawings accompany each plant treated. The technical descriptions are somewhat brief, but the illustrations provide enough detail that field identification can be made easily in most cases. Perhaps one of the most valuable sections is the annotated plant list included at the end of the book. In an easy-to-read format, a great deal of information is concisely summarized for over 300 plants. The chart is subdivided into 7 general categories of plant use (i.e., food and beverage, medicine, construction, etc.), with information given on how each plant is used by specific pueblos. The chart is well referenced and includes original citations for every use.

A brief, yet well-organized analysis of the changes in plant utilization that occurred with the Spanish colonization in the Southwest is provided in chapter 3. The authors take a very complex history and present it in the context of plant ecology. It provides an informative view of the ecological consequences of the collision of cultures. Contemporary culture, plant use, and ecological modification are also included in this text. Two chapters provide insightful information on current cultural and ecological issues. Throughout the text, and reflected in the annotated plant list as well, the authors have attempted to treat religious and ceremonial plant uses with appropriate respect. An added benefit of the book is the authors' personal association with individuals in different Pueblo tribes. Their sense of respect and honor for these cultures is felt throughout the book.

Our only complaint relating to this text is the lack of references citing specific information. It is quite difficult to identify references for much of the information included within the text, with the exception of the chapter discussing indicator species. A bibliography with

145 references is included at the end of the book, but it is difficult to relate these references to particular chapters and specific information. This omission weakens the usefulness of the book as a reference for serious students. It may be that the authors consciously omitted citations in an effort to allow the text to flow more easily, but it is a constant frustration when one is interested in identifying sources. A list of suggested reading is included at the end of each chapter, but no reference is given to original sources that support specific facts. In the preface, the authors do mention many sources that contribute in a general way.

Overall, this book is one that should be included in a field book box, on the bookcase as a reference for plants and their uses by cultures of the Southwest, and in a travel file as it gives suggestions for specific hikes located in the Pueblo Province. For anyone interested in plant ecology, taxonomy, ethnobotany, cultural anthropology, or simply those with a general love for the Southwest, this book is highly recommended. It is well written, informative, and aesthetically delightful.

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BIOGEOGRAPHIC SIGNIFICANCE OF LOW-ELEVATION RECORDS FOR *NEOTOMA CINEREA* FROM THE NORTHERN BONNEVILLE BASIN, UTAH

Donald K. Grayson[1], Stephanie D. Livingston[2], Eric Rickart[3], and Monson W. Shaver III[4]

ABSTRACT.—The existence of low-elevation populations of *Neotoma cinerea* in the northern Bonneville Basin shows either that these mammals can survive many thousands of years in xeric habitats or that they can move across xeric lowlands far more readily than has been appreciated, or both. Current models of Great Basin small mammal biogeography are far too static to encompass properly the interaction of the wide range of geographical and biological variability that has produced the modern distribution of those mammals that have, for several decades, been treated as "montane" within the Great Basin.

Key words: Great Basin, biogeography, island biogeography, Neotoma cinerea, *mammals.*

Ever since J. H. Brown's insightful analyses of Great Basin small mammal biogeography (Brown 1971, 1978, see also Lomolino et al. 1989), biogeographers have treated the bushy-tailed woodrat (*Neotoma cinerea*) as a member of an assemblage of small mammals that is currently isolated on Great Basin mountains. The composition of this assemblage is of particular importance because it has been used to generate and test hypotheses about the past and future of Great Basin "montane" mammals (e.g., Grayson 1987, 1993, Patterson 1990, Cutler 1991, McDonald and Brown 1992, Murphy and Weiss 1992, Grayson and Livingston 1993). However, there is a growing body of data that suggests that this group of mammals lacks the coherence that has been assigned to it. Here, we add to that growing body and call for a more dynamic view of Great Basin small mammal historic biogeography.

NEOTOMA CINEREA ON HOMESTEAD KNOLL, UTAH

Located a few km west and south of Great Salt Lake in north central Utah, the Lakeside Mountains are formed from a complex of north-trending hills, ridges, knolls, and small mountains (Fig. 1). The northwestern-most spur of this complex is Homestead Knoll, a low (maximum elevation 1615 m), rocky promontory that is devoid of active springs and permanent

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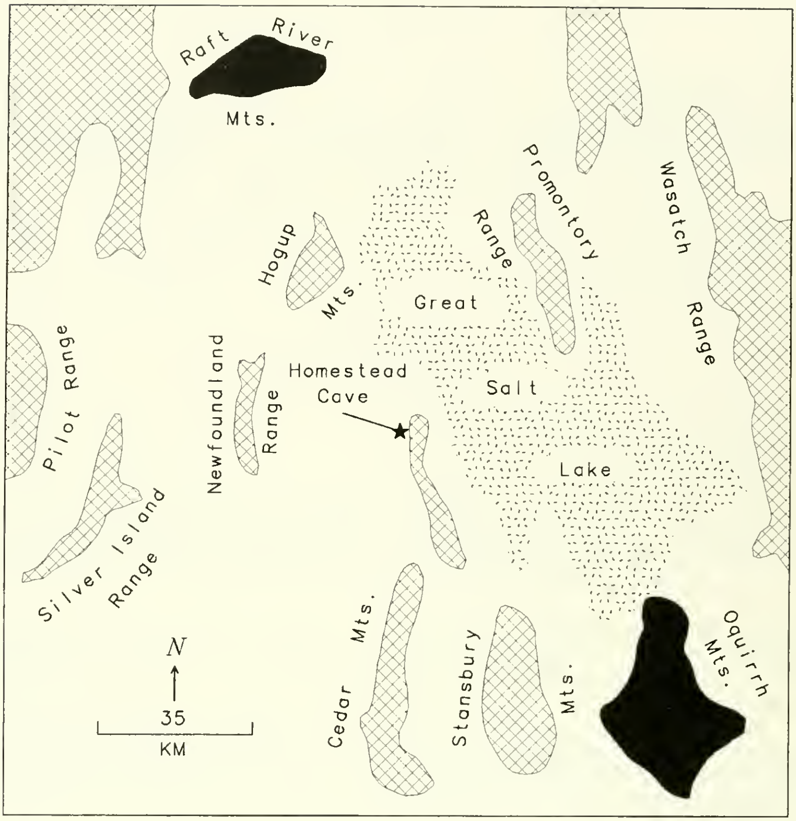

Fig. 1. Location of Homestead Cave within the northern Bonneville Basin.

streams, and that is separated from other parts of the Lakeside group by valleys whose maximum elevations do not exceed 1465 m.

The barren playa of Pleistocene Lake Bonneville is located to the immediate west and northwest of Homestead Knoll. Vegetation of the knoll is dominated by shrubs and grasses, although there are a few scattered Utah junipers (*Juniperus osteosperma*) on its highest reaches.

Most prominent among the shrubs are *Atriplex confertifolia*, *Tetradymia spinosa*, and *Tetradymia glabrata*. *Artemisia tridentata* is present along seasonally moist drainages, while *Artemisia spinescens*, *Chrysothamnus* sp., and *Sarcobatus vermiculatus* are present but uncommon above the flanks of the knoll. *Artemisia nova* occurs on those flanks as does *Ceratoides lanata*, while *S. vermiculatus* becomes increasingly abundant as the valley bottoms are approached. We made no attempt to identify the grasses that form the understory beneath the shrubs, but cheatgrass (*Bromus tectorum* and, perhaps, *B. rubens*) is extremely abundant on the flats beneath the knoll.

Homestead Knoll is dotted by a number of caves, one of which, Homestead Cave, sits on the northwestern edge of the knoll at an elevation of 1406 m (Fig. 2). Approximately 11 m wide and 6 m high at its mouth, this 25-m-deep cave has, since 1992, been the focus of interdisciplinary paleoecological work funded by the Department of Defense. With D. B. Madsen of the Utah Geological Survey, 3 authors of this paper (DKG, SDL, and MWS) have been involved with the excavation and analysis of a deep sequence of vertebrate remains from this site. To provide background data for the analysis of the mammalian component of the excavated fauna, we conducted a brief (270 trap-night) small mammal survey in the vicinity of Homestead Cave in June 1995.

With 1 exception, the results of this survey were quite predictable. Trapping success was low, with 3 species—*Dipodomys ordii* (3 individuals), *Peromyscus maniculatus* (11 individuals), and *Neotoma lepida* (6 individuals)—comprising nearly the entire trapped assemblage. The 1 exception, however, was remarkable: we

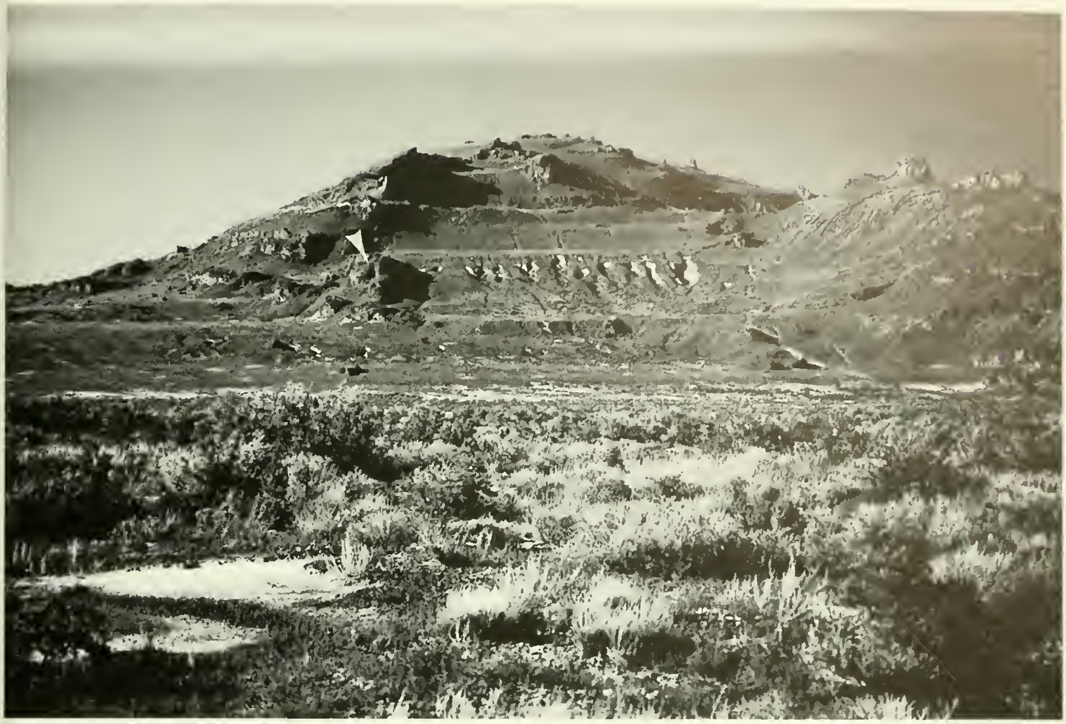

Fig. 2. Location of Homestead Cave (white arrow) on Homestead Knoll; the prominent terraces represent Provo, post-Provo regressive, and Stansbury beaches left by the waters of Pleistocene Lake Bonneville.

took a single *Neotoma cinerea* from the back of Homestead Cave itself.

Because this individual was live-trapped and released, we cannot report its age or sex or provide standard measurements. Even though we do not have a voucher specimen, we do have an excellent videotape of the animal (taken by MWS and on file at the Utah Geological Survey), and there is no doubt as to the identification of the individual.

Vegetation in the immediate vicinity of Homestead Cave departs from the Homestead Knoll vegetation that we have described in only 1 major way: the mouth of the cave supports a luxuriant growth of *Ribes cereum* immediately beneath the dripline. It would be surprising if this shrub were not heavily utilized by both *Neotoma cinerea*, taken at the rear of the cave, and *Neotoma lepida*, taken at the front.

OTHER LOW-ELEVATION NORTHERN BONNEVILLE BASIN RECORDS FOR *NEOTOMA CINEREA*

Our discovery of *Neotoma cinerea* on Homestead Knoll led us to search the mammal collection at the Utah Museum of Natural History, University of Utah, for additional records of this species from other low-elevation settings in the northern Bonneville Basin. We were quite successful in this search:

(a) **Locomotive Springs:** The only previously published low-elevation record for *Neotoma cinerea* for the northern Bonneville Basin was provided by Durrant (1952:348; UU 5048) as having been taken in October 1947 from "Statehouse, Locomotive Springs, 5500 ft. [1676 m]." However, we are unable to determine the location of "Statehouse" and are otherwise hesitant to accept this record because of the substantial difference between the actual elevation of Locomotive Springs (1283 m) and the reported elevation of "Statehouse" (1676 m). Given the well-watered nature of Locomotive Springs, the record might be accurate, but it is in need of verification. Locomotive Springs is approximately 60 km north of Homestead Knoll.

(b) **Lakeside Mountains:** An adult male *Neotoma cinerea* (UU 14374) was collected "5 mi. E Lakeside, 4600 ft. [1402 m]" in June 1957. This distance and direction from Lakeside, however, describe a point in the Great Salt Lake. If the actual direction were southeast, the specimen could have come from Cave Ridge on the eastern edge of the Lakeside Mountains, approximately 10 km east of Homestead Knoll.

(c) Newfoundland Mountains: A series of three juvenile *Neotoma cinerea* (UU 9995, 9996, 9998) were collected in June 1951 from an unspecified site at the north end of the Newfoundland Mountains. The collector's field notes do not provide the elevation of the site but do indicate that the specimens came from an area of granite cliffs with a plant community that included *Juniperus* and *Tetradymia.* The north end of the Newfoundland Mountains is approximately 40 km west-northwest of Homestead Knoll.

(d) Cedar Mountains: There are records for *Neotoma cinerea* from 2 separate locations in the southern Cedar Mountains: 4 from the Cane Springs area (elevation 1768 m; UU 26340, 27297, 27299, and 27301-2, collected between October 1952 and January 1953), and 1 from the "south end Cedar Mtn., 4850 ft. [1478 m]." This last specimen is reported to have been caught in a garage, suggesting that it may have come from near Dugway. Although these specimens come from no closer than 95 km to the south of Homestead Cave, we mention them because they establish the likelihood that *Neotoma cinerea* occurs in suitable habitat throughout the Cedar Range.

BIOGEOGRAPHIC CONSIDERATIONS

Although *Neotoma cinerea* has frequently been treated as being isolated on Great Basin mountains (Brown 1971, 1978, Grayson 1993), these records demonstrate that bushy-tailed woodrats can and do exist at low elevations in arid contexts within at least the northern Bonneville Basin. How, one must wonder, did *Neotoma cinerea* come to occupy such arid, low-elevation settings as the Newfoundland Mountains (maximum elevation 2130 m) and isolated knolls on the Lakeside Mountains (maximum elevation 2020 m)?

It is well established that during the late Pleistocene, bushy-tailed woodrats were far more widely distributed within the Great Basin than they are today, occupying low-elevation settings where they are no longer found (Grayson 1988, 1993). As a result, it is reasonable to speculate that these animals were also widespread in this part of the northern Bonneville Basin during those years. We can, however, do much more than speculate about the history of *N. cinerea* in the Homestead Knoll area.

With a maximum elevation of 1615 m, Homestead Knoll was covered by the waters of Pleistocene Lake Bonneville 14,500 years B.P., when Pleistocene Lake Bonneville was at its high (see Figure 2). Obviously, Homestead Knoll must have received its woodrats after this time, but when this occurred is not clear. Between 14,500 and at least 14,200 years B.P., when Lake Bonneville stood at the Provo level, Homestead Knoll was an island of approximately 770 acres. Not until Lake Bonneville fell to a local elevation of 1463 m did this island become connected to the main body of the Lakeside Mountains. Once this occurred, Homestead Knoll became part of the faunal mainland and would have been open to overland colonization by terrestrial mammals.

Unfortunately, we do not know when the lake fell to this level. However, we do have direct evidence from Homestead Cave concerning the regional history of *Neotoma cinerea.* Excavations in this cave have provided a rich, stratified sequence of vertebrate remains, the mammals of which are being identified and analyzed by one of the authors (DKG). To date, a substantial sample of mammal specimens from the 4 lowest Homestead Cave strata has been identified (37,381 specimens).

All 4 assemblages contain both *N. cinerea* and *N. lepida,* but the ratio of *N. cinerea* to *N. lepida* varies dramatically through time. In stratum I, which dates to between ca 11,300 and 10,000 years B.P., bushy-tailed woodrats make up 99.38% of the *Neotoma* fauna. In subsequent strata, however, they decline steadily in abundance; by stratum IV (ca 8200–7200 years B.P.), *N. cinerea* comprises only 4.74% of the *Neotoma* assemblage (Fig. 3). Similarly, *N. cinerea* contributes 23.97% of the total number of identified mammalian specimens in stratum I, a number that declines to 1.01% in stratum IV (Fig. 4).

The Homestead Cave fauna thus documents that *N. cinerea* was present in the Homestead Knoll area by 11,300 years B.P. and remained a common species in the small mammal fauna through much of the Early Holocene. After ca 8200 years B.P., however, *N. lepida* became the overwhelmingly dominant member of the genus, and *N. cinerea* became locally rare. Since mammals from later strata within Homestead Cave

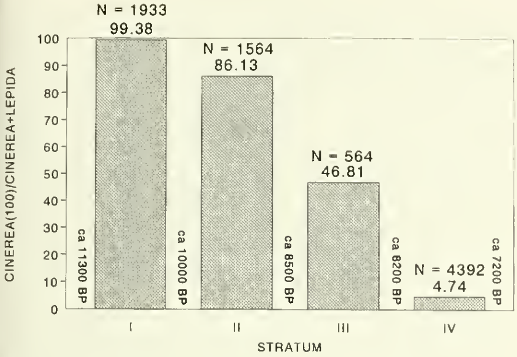

Fig. 3. Changing contribution of *N. cinerea* to the *Neotoma* (*N. cinerea* plus *N. lepida*) fauna, Homestead Cave strata I–IV (N = total number of *Neotoma* specimens identified to the species level, including those identified as *N.* cf. *cinerea* and *N.* cf. *lepida*).

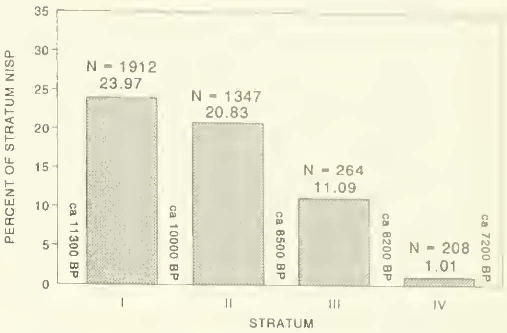

Fig. 4. Changing contribution of *Neotoma cinerea* to the total number of identified mammalian specimens (NISP) per stratum at Homestead Cave, strata I–IV.

have not yet been completely identified, we do not know whether *N. cinerea* survived the very xeric Middle Holocene (ca 7500–5000 years B.P.) here.

Currently, there are 2 options for explaining the modern existence of *N. cinerea* on Homestead Knoll. First, animals living here today may be direct descendants of the initial woodrat colonizers of the knoll, colonizers that arrived sometime between 14,500 and 11,300 years B.P. If so, the population has survived even though its numbers dropped precipitously toward the end of the Early Holocene (ca 8200–7200 years B.P.), and presumably fell even further during the heart of the Middle Holocene. Assuming that *N. cinerea* does not now survive in the valleys that separate Homestead Knoll from nearby uplands, and that it has not been able to survive in those valleys since at least 7000 years B.P., then this population has existed on an isolated upland a few thousand acres in extent for a minimum of some 7 millennia.

The other, and certainly more likely, option is that *Neotoma cinerea* has not been isolated on Homestead Knoll for this entire period of time, that populations on the knoll have been augmented by immigrants from elsewhere, and that any local extinctions of *N. cinerea* on the knoll have been followed by recolonizations from nearby populations. Indeed, it is even possible that the current representatives of the species colonized Homestead Knoll during the mid-1980s, a time of extraordinarily high precipitation in the northern Great Basin (Arnow and Stephens 1990).

IMPLICATIONS

The discovery of *Neotoma cinerea* on Homestead Knoll does not simply represent an unexpected natural historical tidbit. Our discovery documents either that populations of *Neotoma cinerea* within the Great Basin can find sufficient refuge in low-elevation, xeric habitats to survive for many thousands of years, or that this species can move across xeric lowlands far more readily than has been appreciated, or both. Indeed, insofar as bushy-tailed woodrats are more effective colonizers than has been realized, an effective parallel may exist in the yellow-nosed cotton rat (*Sigmodon ochrognathus*), a "montane" mammal of the Southwest that has apparently expanded its range across low-elevation valleys during the past 50 years (Davis and Dunford 1987; see also Davis and Callahan [1992] on *Microtus mexicanus*).

Elsewhere, Grayson and Livingston (1993) have noted that *Sylvilagus nuttallii* can cross valley bottoms in at least parts of the Great Basin. Now, it seems that *N. cinerea* can survive in habitats that are anything but montane. This fact leads us to suggest that the nestedness of Great Basin mammal faunas (sensu Patterson and Atmar 1986, Patterson 1987, 1990) might reflect a combination of extinction histories *and* colonization abilities. In addition, the Homestead Knoll record for *N. cinerea* takes its place alongside other recent data documenting that current models of Great Basin small mammal biogeography are far too static to encompass properly the wide range of geographical and biological variability that has produced the modern distribution of those mammals that, for several decades, have been treated as "montane" within the Great Basin (e.g., Grayson 1993, Grayson and Livingston 1993, Lawlor 1995, Rickart 1995). In the Southwest, modern montane mammal distributions have clearly been determined by a complex combination of Holocene extinctions and colonizations (e.g., Davis and Dunford 1987, Lomolino et al. 1989, Davis and Callahan 1992). It now appears that the situation in the Great Basin is quite similar.

ACKNOWLEDGMENTS

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SYNOPSIS OF THE MOSSES OF WYOMING

P. M. Eckel[1]

ABSTRACT.—A revised list of the mosses of the State of Wyoming is presented. Recorded are 315 species and varieties.

Key words: bryophytes, Wyoming, Porter, Rocky Mountains, checklist, flora.

Publication of the mosses of Wyoming began with Aven Nelson (1900) listing 119 species. His collections were made essentially in the Laramie and Medicine Bow ranges of Carbon and Albany counties, and his specimens are now at the Rocky Mountain Herbarium (RM). Nelson's specimens were determined in large part by Professor John M. Holzinger, of the State Normal School at Winona, Minnesota. Aven Nelson's and Elias Nelson's Wyoming collections were distributed under printed labels as "Plants of Wyoming from the Rocky Mountain Herbarium" and "Plants of Yellowstone National Park from the Rocky Mountain Herbarium," citing Holzinger and a few others as determiners. However, because they were issued without serial numbers, showing only the collectors' numbers together with other data, they do not constitute true exsiccatae (Sayre 1971).

In 1935 Cedric Lambert Porter published a valuable checklist of the mosses of the State of Wyoming, citing 215 species and varieties. In this publication Porter mentioned a paper by Dwight C. Smiley on the mosses of Yellowstone National Park, which Porter cited again two years later as "A Key to the Mosses of Yellowstone National Park" [unpublished] (Porter 1937). Porter included Smiley's names but apparently did not examine his specimens.

The substance of a dissertation written by Porter at the University of Washington in 1937 was the development of a useful key to the hepatic and bryophyte taxa of Wyoming. It includes additional county records, a few additional species, and references to Yellowstone National Park, again apparently citing Smiley's unpublished material. On a recent visit to the Yellowstone National Park Herbarium (YELLO), I was able to locate and borrow for study some of Mr. Smiley's specimens. Several were determined by R. S. Williams.

No checklist focusing on the moss flora of Yellowstone National Park has as yet been published. The 357 or so moss specimens curated at YELLO all derive from the park. The following are collectors and dates of collecting activity: Dwight Smiley, 1932; H. S. Conard, 1948; Winona Welch, 1951; Eula Whitehouse, 1951; Elva Lawton, 1953. No biographical data exist on Mr. Smiley at YELLO (Whipple personal communication). I have no other record that these collectors worked in Wyoming, but my use of various herbaria for this checklist is not exhaustive. Incidentally, there are 11 packets of liverworts at YELLO, and no representation of *Sphagnum*.

Recent collectors in the state include the late Fredrick Hermann, Holmes Rolston, and William Weber, all of whose Wyoming specimens are distributed in various herbaria, especially COLO. Steven Churchill (1979, 1982), John Spence (1985), and Alvin L. Medina (1994) collected additional taxa. Two taxa listed here as new to the state were recently collected by Joseph Elliott (*Scorpidium scorpioides* and *Cinclidium stygium*). General references to extensive collections made in the state are given by Lawton (1971).

The purpose of this paper is to present an up-to-date list of the mosses of the State of Wyoming, incorporating reports published since Porter's manuscripts as well as additional unpublished information. There are 315 species and varieties in the present list. Some idea of the degree of representation of the flora of Wyoming comprising this list may be inferred from a glance at similar checklists for other areas. It is probably to be expected that the arid intermountain states, such as Utah and Nevada, will have a more depauperate flora; Spence (1988) recorded 342 species for the entire Intermountain West. The following counts are for species and varieties (except Utah which is species only): Arizona 381 (Johnsen, no date), Colorado 292 (Weber 1973), Idaho 257 (McCleary and Green 1971), Montana 358 (Eversman and Sharp 1980), Nevada 165 (Lawton 1958, Lavin 1981), Oregon 441 (Christy et al. 1982), Utah 256 (Flowers 1973). There appears to be no checklist for the state of Washington. New York State, which is said to have a diverse moss flora, has 503 species and varieties (Ketchledge 1980). A striking comparison is to the oceanic island of Newfoundland, which boasts a moss flora of 445 species (Brassard 1983) and which is geophysiographically rather plain compared to the geomorphic extremes and diversity of Wyoming in the Central Rocky Mountains.

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[1] Clinton Herbarium, Buffalo Museum of Science, Buffalo, NY 14214.

The following checklist is based largely on a review of specimens housed in the Rocky Mountain Herbarium. Additional herbaria were contacted in instances of taxa reported in the literature but with no representation at RM, and numerous new records have been added from field collections by myself and others. I have attempted to cite at least one reliable specimen of each taxon by giving the abbreviation of the herbarium at which the specimen is located. Additional taxa are added from Porter's 1937 dissertation if they did not occur in his previous publication. If a herbarium designation is noted below for a taxon, no further reference to the literature is given. Although several references to the same species throughout the literature may have been cited, only one citation is presented for names for which specimens have not been seen.

Nomenclature other than *Sphagnum* follows Anderson et al. (1990). *Sphagnum* nomenclature follows Anderson (1990).

Families are given alphabetically, genera alphabetically within families, and species alphabetically within genera.

CHECKLIST OF MOSSES OF WYOMING

AMBLYSTEGIACEAE

Amblystegium serpens (Hedw.) Schimp. var. *serpens* (NY, RM)
    var. *juratzkanum* (Schimp.) Rau & Herv. (RM)
Amblystegium varium (Hedw.) Lindb. (NY, RM)
Calliergon cordifolium (Hedw.) Kindb. (TENN)
Calliergon giganteum (Schimp.) Kindb. (NY)
Calliergon richardsonii (Mitt.) Kindb. *in* Warnst. (Lawton 1971)
Calliergon stramineum (Brid.) Kindb. (COLO, RM)
Calliergon trifarium (Web. & Mohr) Kindb. (Cooper and Andrus 1994)
Calliergonella cuspidata (Hedw.) Loeske (WTU)
Campylium chrysophyllum (Brid.) J. Lange (BUF, RM)
Campylium hispidulum (Brid.) Mitt. (NY)
Campylium polygamum (Schimp. *in* BSG) C. Jens. (RM)
Campylium stellatum (Hedw.) C. Jens. (RM)
Conardia compacta (C. Muell.) Robins. (NY, WTU)
Cratoneuron filicinum (Hedw.) Spruce (NY, RM)
Drepanocladus aduncus (Hedw.) Warnst. var. *aduncus* (RM)
    var. *kneiffii* (Schimp. *in* BSG) Moenk. (RM)
    var. *polycarpus* (Bland. *ex* Voit) Roth (COLO, RM)
Drepanocladus capillifolius (Warnst.) Warnst. (RM)
Drepanocladus crassicostatus Janssens (CANM)
Drepanocladus sendtneri (Schimp.) Warnst. (BING)
Hygroamblystegium noterophilum (Sull. & Lesq. *in* Sull.) Warnst. (RM)
Hygroamblystegium tenax (Hedw.) Jenn. (RM)
Hygrohypnum bestii (Ren. & Bryhn *in* Ren.) Broth. (WTU)
Hygrohypnum duriusculum (De Not.) Jamieson (CSU)
Hygrohypnum luridum (Hedw.) Jenn. (NY, RM)
Hygrohypnum molle (Hedw.) Loeske (RM, WTU)
Hygrohypnum ochraceum (Turn. *ex* Wils.) Loeske (BUF, CSU, RM)
Hygrohypnum smithii (Sw. *in* Lilj.) Broth. (RM)
Leptodictyum humile (P. Beauv.) Ochyra (RM)
Leptodictyum riparium (Hedw.) Warnst. (NY, RM)
Limprichtia revolvens (Sw.) Loeske (BING, BUF)
Palustriella commutata (Brid.) Ochyra (RM, WTU)
Palustriella decipiens (De Not.) Ochyra (RM, WTU)
Pseudocalliergon turgescens (T. Jens.) Loeske (COLO, RM)
Sanionia uncinata (Hedw.) Loeske (NY, RM)
Sarmenthypnum sarmentosum (Wahlenb.) Tuom. & T. Kop. (BING, COLO, RM)
Scorpidium scorpioides (Hedw.) Limpr. (BUF)
Warnstorfia exannulata (Schimp. *in* BSG) Loeske
    var. *exannulata* (CSU, RM)
Warnstorfia fluitans (Hedw.) Loeske (COLO, RM)

ANDREAEACEAE

Andreaea rupestris Hedw. (YELLO)

AULACOMNIACEAE

Aulacomnium androgynum (Hedw.) Schwaegr. (TENN)
Aulacomnium palustre (Hedw.) Schwaegr. (BUF, RM, TENN)

BARTRAMIACEAE

Anacolia menziesii (Turn.) Par. (WTU)
Bartramia ithyphylla Brid. (RM)
Philonotis fontana (Hedw.) Brid. var. *fontana* (BUF, RM)
    var. *americana* (Dism.) Flow. (BUF, RM)
    var. *caespitosa* (Jur.) Schimp. (BUF, RM)
    var. *pumila* (Turn.) Brid. (RM)

BRACHYTHECIACEAE

Brachythecium acutum (Mitt.) Sull. (RM)
Brachythecium albicans (Hedw.) Schimp. *in* BSG (RM)

Brachythecium collinum (Schleich. *ex* C. Muell.) Schimp. *in* BSG (BUF, NY, RM)
Brachythecium erythrorrhizon Schimp. *in* BSG (RM)
Brachythecium fendleri (Sull.) Jaeg. (RM)
Brachythecium frigidum (C. Muell.) Besch. (NY, US)
Brachythecium leibergii Grout (NY, RM, US)
Brachythecium nelsonii Grout (CSU, NY, RM)
Brachythecium oedipodium (Mitt.) Jaeg. (COLO, RM, US)
Brachythecium rivulare Schimp. *in* BSG (NY, RM, US)
Brachythecium rutabulum (Hedw.) Schimp. *in* BSG (NY)
Brachythecium salebrosum (Web. & Mohr) Schimp. *in* BSG (BUF, RM, US)
Brachythecium starkei (Brid.) Schimp. *in* BSG (Porter 1935)
Brachythecium turgidum (C.J. Hartm.) Kindb. (COLO, NY, RM, US)
Brachythecium velutinum (Hedw.) Schimp. *in* BSG
 var. *velutinum* (Spence 1985)
 var. *venustum* (De Not.) Arc. (BUF, RM)
Cirriphyllum cirrosum (Schwaegr. *in* Schultes) Grout (NY)
Eurhynchium oreganum (Sull.) Jaeg. (Spence 1985)
Eurhynchium pulchellum (Hedw.) Jenn. (RM)
Homalothecium aeneum (Mitt.) Lawt. (RM, US)
Homalothecium nevadense (Lesq.) Ren. & Card. (US)
Homalothecium pinnatifidum (Sull. & Lesq.) Lawt. (BUF, RM)
Tomentypnum nitens (Hedw.) Loeske (COLO, RM)

BRYACEAE

Bryum algovicum Sendtn. *ex* C. Muell. (BUF, RM, US)
Bryum alpinum Huds. *ex* With. (Porter 1935)
Bryum amblyodon C. Muell. (Spence 1985)
Bryum arcticum (R. Br.) Bruch & Schimp. *in* BSG (Lawton 1971)
Bryum argenteum Hedw. (RM)
Bryum caespiticium Hedw. (RM, US)
Bryum capillare Hedw. (RM, US)
Bryum cyclophyllum (Schwaegr.) Bruch & Schimp. *in* BSG (RM, WTU)
Bryum dichotomum Hedw. (Spence 1985)
Bryum lisae De Not. var. *cuspidatum* (Bruch & Schimp. *in* BSG) Marg. (RM)
Bryum pallescens Schleich. *ex* Schwaegr. (RM)
Bryum pseudotriquetrum (Hedw.) Gaertn., Meyer & Scherb. (RM)
Bryum turbinatum (Hedw.) Turn. (NY, RM)
Bryum uliginosum (Brid.) Bruch & Schimp. *in* BSC (Spence 1985)
Bryum weigelii Spreng. *in* Biehler (RM)
Leptobryum pyriforme (Hedw.) Wils. (RM)
Pohlia andalusica (Hoehn.) Broth. (Shaw 1981)
Pohlia bolanderi (Sull.) Broth. var. *seriata* Shaw (CSU, RM)
Pohlia camptotrachela (Ren. & Card.) Broth. (Shaw 1981)
Pohlia cruda (Hedw.) Lindb. (BUF, RM)
Pohlia drummondii (C. Muell.) Andr. (WTU)
Pohlia elongata Hedw. (Porter 1935)
Pohlia lescuriana (Sull.) Grout (Porter 1935)
Pohlia longicolla (Hedw.) Lindb. (RM)
Pohlia ludwigii (Schwaegr. *ex* Schwaegr.) Broth. (RM)
Pohlia nutans (Hedw.) Lindb. (BUF, CSU, RM)
Pohlia obtusifolia (Brid.) L. Koch. (COLO, RM)
Pohlia proligera (Kindb. *ex* Brid.) Lindb. *ex* Arnell (BUF)
Pohlia tundrae Shaw (BUF, RM)
Pohlia wahlenbergii (Web. & Mohr) Andrews (RM)
Roellia roellii (Broth. *in* Roell) Andrews *ex* Crum (RM, WTU)

BUXBAUMIACEAE

Buxbaumia aphylla Hedw. (WTU)
Buxbaumia viridis (DC.) Moug. & Nestl. (WTU)

CLIMACIACEAE

Climacium americanum Brid. (BING, BUF)
Climacium dendroides (Hedw.) Web. & Mohr (COLO, CSU, RM)
Climacium kindbergii (Ren. & Card.) Grout (Porter 1935)

DICRANACEAE

Campylopus fragilis (Brid.) Bruch & Schimp. *in* BSG (WTU)
Cynodontium alpestre (Wahlenb.) Milde (Lawton 1971)
Cynodontium polycarpon (Hedw.) Schimp. (Porter 1935)
Cynodontium schisti (Web. & Mohr) Lindb. (Porter 1935)
Dichodontium olympicum Ren. & Card. (RM)
Dichodontium pellucidum (Hedw.) Schimp. (RM)
Dicranella schreberiana (Hedw.) Hilf. *ex* Crum & Anderson (RM)
Dicranella subulata (Hedw.) Schimp. (RM)
Dicranoweisia cirrata (Hedw.) Lindb. *ex* Milde (RM)
Dicranoweisia crispula (Hedw.) Lindb. *ex* Milde (COLO, RM)
Dicranum bonjeanii De Not. *in* Lisa (Porter 1937)
Dicranum muehlenbeckii Bruch & Schimp. *in* BSG (COLO, RM)
Dicranum polysetum Sw. (Wynne 1943, Ireland 1982)
Dicranum rhabdocarpum Sull. (RM)
Dicranum scoparium Hedw. (RM)
Dicranum spadiceum Zett. (COLO, RM)
Dicranum tauricum Sapehin (RM)
Oncophorus virens (Hedw.) Brid. (RM)
Oncophorus wahlenbergii Brid. (COLO, RM)
Paraleucobryum enerve (Thed. *in* Hartm.) Loeske (COLO, RM)

DITRICHACEAE

Ceratodon purpureus (Hedw.) Brid. (BUF, RM)
Distichum capillaceum (Hedw.) Bruch & Schimp. *in* BSG (BUF, RM)
Distichum inclinatum (Hedw.) Bruch & Schimp. *in* BSG (NY, RM)
Ditrichum flexicaule (Schwaegr.) Hamp. (RM)
Saelania glaucescens (Hedw.) Broth. *in* Bomanss. & Broth. (WTU)

ENCALYPTACEAE

Encalypta alpina Sm. (Porter 1937)
Encalypta ciliata Hedw. (Porter 1937, Horton 1983)
Encalypta procera Bruch (Porter 1937)
Encalypta rhabdocarpa Schwaegr. (RM)
Encalypta vulgaris Hedw. (RM)

FISSIDENTACEAE

Fissidens adianthoides Hedw. (WTU)
Fissidens bryoides Hedw. (RM, WTU)
Fissidens grandifrons Brid. (BUF, RM, WTU)
Fissidens obtusifolius Wils. var. *marginatus* Flow. (NY)
Fissidens osmundioides Hedw. (WTU)

FONTINALACEAE

Dichelyma falcatum (Hedw.) Myr. (COLO, RM)
Dichelyma uncinatum Mitt. (WTU)
Fontinalis antipyretica Hedw. var. *antipyretica* (RM, WTU)
  var. *gigantea* (Sull.) Sull. (RM)
  var. *oregonensis* Ren. & Card. (RM, WTU)
Fontinalis hypnoides Hartm. var. *hypnoides* (RM)
  var. *duriaei* (Schimp.) Husn. (RM)
Fontinalis neomexicana Sull. & Lesq. (RM)

FUNARIACEAE

Funaria flavicans Michx. (Porter 1935)
Funaria hygrometrica Hedw. (RM)
Physcomitrium hookeri Hampe (TENN)

GRIMMIACEAE

Coscinodon calyptratus (Hook. *in* Drumm.) C. Jens *ex* Kindb. (RM)
Grimmia affinis Hoppe & Hornsch. *ex* Hornsch (RM)
Grimmia anodon Bruch & Schimp. *in* BSG (NY, RM)
Grimmia anomala Hampe *ex* Schimp. (Lawton 1971)
Grimmia donniana Sm. (Wynne 1943)
Grimmia elatior Bruch *ex* Bals. & De Not. (RM)
Grimmia laevigata (Brid.) Brid. (Porter 1935)
Grimmia montana Bruch & Schimp. *in* BSG (RM)
Grimmia ovalis (Hedw.) Lindb. (RM)
Grimmia plagiopodia Hedw. (RM)
Grimmia pulvinata (Hedw.) Sm. (RM)
Grimmia tenerrima Ren. & Card. (RM)
Grimmia torquata Hornsch. *in* Grev. (CSU)
Grimmia trichophylla Grev. (Lawton 1971, Spence 1985)
Jaffueliobryum wrightii (Sull. *in* Gray) Ther. (Wynne 1943)
Racomitrium canescens (Hedw.) Brid. (COLO, RM, WTU)
Racomitrium lanuginosum (Hedw.) Brid. (Crum and Anderson 1981)
Racomitrium sudeticum (Funck) Bruch & Schimp. *in* BSG (COLO, WTU)
Schistidium agassizii Sull. & Lesq. *in* Sull. (RM)
Schistidium apocarpum (Hedw.) Bruch & Schimp. *in* BSG (NY, RM)
Schistidium occidentale (Lawt.) Churchill (Lawton 1971) (RM)
Schistidium rivulare (Brid.) Podp. var. *rivulare* (RM)
  var. *latifolium* (Zett.) Crum & Anderson (BUF)
Schistidium tenerum (Zett.) Nyh. (RM)
Scouleria aquatica Hook. *in* Drumm. (RM)

HEDWIGIACEAE

Hedwigia ciliata (Hedw.) P. Beauv. (BUF, RM)

HELODIACEAE

Helodium blandowii (Web. & Mohr) Warnst. (BUF, RM)

HYLOCOMIACEAE

Hylocomium splendens (Hedw.) Schimp. *in* BSG (RM)
Pleurozium schreberi (Brid.) Mitt. (WTU)
Rhytidiadelphus triquetrus (Hedw.) Warnst. (RM)

HYPNACEAE

Hypnum cupressiforme Hedw. var. *cupressiforme* (BUF, NY, RM)
  var. *resupinatum* (Tayl.) Schimp. *in* Spruce (Porter 1935)
Hypnum lindbergii Mitt. (RM)
Hypnum pallescens (Hedw.) P. Beauv. (RM)
Hypnum revolutum (Mitt.) Lindb. (RM)
Hypnum vaucheri Lesq. (LAF)
Isopterygiopsis pulchella (Hedw.) Iwats. (RM)
Platydictya jungermannioides (Brid.) Crum (RM)
Ptilium crista-castrensis (Hedw.) De Not. (WTU)
Pylaisiella polyantha (Hedw.) Grout (Porter 1935)

LESKEACEAE

Pseudoleskea incurvata (Hedw.) Loeske (CSU, RM)
Pseudoleskea patens (Lindb.) Kindb. (RM)
Pseudoleskea radicosa (Mitt.) Macoun & Kindb. (RM)
  var. *compacta* Best (Lawton 1971)
  var. *pallida* (Best) Crum, Steere & Anderson (Lawton 1971)
Pseudoleskea stenophylla Ren. & Card. *in* Roell. (Spence 1985)
Pseudoleskeella tectorum (Funck *ex* Brid.) Kindb. *in* Broth. (NY, RM, WTU)

MEESIACEAE

Amblyodon dealbatus (Hedw.) Bruch & Schimp. *in* BSG (WTU)
Meesia uliginosa Hedw. (RM)

MNIACEAE

Cinclidium stygium Sw. *in* Schrad. (BUF, NYS)
Mnium ambiguum H. Muell. (RM)
Mnium arizonicum Amann (CSU, RM)
Mnium blyttii Bruch & Schimp. *in* BSG (RM)
Mnium marginatum (With.) Brid. *ex* P. Beauv. (RM)
Mnium spinulosum Bruch & Schimp. *in* BSG (Porter 1935, Spence 1985)
Mnium thomsonii Schimp. (RM)
Plagiomnium ciliare (C. Muell.) T. Kop. (RM)
Plagiomnium cuspidatum (Hedw.) T. Kop. (RM)
Plagiomnium drummondii (Bruch & Schimp.) T. Kop. (RM)
Plagiomnium ellipticum (Brid.) T. Kop. (RM)
Plagiomnium medium (Bruch & Schimp. *in* B. S. G.) T. Kop. (BUF, RM)
Plagiomnium rostratum (Schrad.) T. Kop. (WTU)
Rhizomnium magnifolium (Horik.) T. Kop. (RM)
Rhizomnium pseudopunctatum (Bruch & Schimp.) T. Kop. (RM)
Rhizomnium punctatum (Hedw.) T. Kop. (Porter 1935, Spence 1985)

NECKERACEAE

Neckera pennata Hedw. (RM)

ORTHOTRICHACEAE

Amphidium lapponicum (Hedw.) Schimp. (CSU)
Orthotrichum affine Brid. (Porter 1935)
Orthotrichum alpestre Hornsch. *in* BSG (RM)
Orthotrichum anomalum Hedw. (NY)
Orthotrichum cupulatum Brid. (NY, RM)
Orthotrichum hallii Sull. & Lesq. *in* Sull. (BUF, RM)
Orthotrichum holzingeri Ren. & Card. *in* Holz (RM)
Orthotrichum laevigatum Zett. (COLO, RM)

Orthotrichum obtusifolium Brid. (MO)
Orthotrichum pellucidum Lindb. (BUF, NY, RM)
Orthotrichum praemorsum Vent. *in* Roell (Porter 1935, Vitt 1973)
Orthotrichum pylaisii Brid. (Vitt 1973)
Orthotrichum rivulare Turn. (Lawton 1971)
Orthotrichum rupestre Schleich. *ex* Schwaegr. (RM)

Plagiotheciaceae

Plagiothecium denticulatum (Hedw.) Schimp. *in* BSG (WTU)
Plagiothecium piliferum (Sw. *ex* Hartm.) Schimp. *in* BSG (Spence 1985)

Polytrichaceae

Atrichum selwynii Aust. (RM, US)
Atrichum undulatum (Hedw.) P. Beauv. (Spence 1985)
Polytrichastrum alpinum (Hedw.) G. L Sm. var. *alpinum* (COLO, RM)
Polytrichum commune Hedw. (RM)
Polytrichum formosum Hedw. (Ireland 1982)
Polytrichum juniperinum Hedw. (RM)
Polytrichum longisetum Brid. (RM)
Polytrichum lyallii (Mitt.) Kindb. (BUF, RM)
Polytrichum piliferum Hedw. (RM)
Polytrichum sexangulare Brid. (RM)
Polytrichum strictum Brid. (RM)

Pottiaceae

Barbula convoluta Hedw. var. *convoluta* (RM)
Barbula unguiculata Hedw. (BUF, LAF)
Bryoerythrophyllum recurvirostre (Hedw.) Chen (BUF, RM, WTU)
Desmatodon cernuus (Hueb.) Bruch & Schimp. *in* BSG (RM, WTU)
Desmatodon guepinii Bruch & Schimp. *in* BSG (BUF, RM)
Desmatodon heimii (Hedw.) Mitt. (BUF, RM)
Desmatodon latifolius (Hedw.) Brid. (TENN, RM, WTU)
Desmatodon leucostoma (R.Br.) Berggr. (WTU)
Desmatodon obtusifolius (Schwaegr.) Schimp. (BUF, RM)
Desmatodon plinthobius (Sull. & Lesq. *in* Sull. (Medina 1994)
Desmatodon porteri James *in* Aust. (Porter 1937)
Desmatodon systylius Schimp. (BUF, RM)
Didymodon asperifolius (Mitt.) Crum, Steere & Anderson (COLO, RM)
Didymodon fallax (Hedw.) Zand. var. *fallax* (RM)
  var. *reflexus* (Brid.) Zand. (Crum and Anderson 1981)
Didymodon rigidulus Hedw. var. *rigidulus* (BUF)
  var. *gracilis* (Schleich. *ex* Hook. & Grev.) Zand. (BUF, NY, RM)
  var. *icmadophilus* (Schimp. *ex* C. Muell.) Zand. (BUF)
Didymodon vinealis (Brid.) Zander var. *vinealis* (BUF, RM)
  var. *flaccidus* (Bruch & Schimp. *in* Schimp.) Zand. (BUF)
  var. *luridus* (Hornsch. *in* Spreng.) Zand. (as *Didymodon trifarius* (Wynne 1943)
  var. *nicholsonii* (Culm.) Zand. (RM)
  var. *rubiginosus* (Mitt.) Zand. (BUF)
Gymnostomum aeruginosum Sm. (BUF, RM, WTU)
Hymenostylium recurvirostre (Hedw.) Dix. (RM, WTU)
Paludella squarrosa (Hedw.) Brid. (Lawton 1971)
Pterygoneurum ovatum (Hedw.) Dix. (BUF, NY, RM)
Pterygoneurum subsessile (Brid.) Jur. (BUF, NY, RM)
Stegonia latifolia (Schwaegr. *in* Schultes) Vent. *ex* Broth. (Lawton 1971)
Tortella fragilis (Hook. & Wils. *in* Drumm.) Limpr. (BUF, LAF, NY, RM, WTU)
Tortella humilis (Hedw.) Jenn. (Spence 1985)
Tortella tortelloides (S. Greene) Robins. (BUF, WTU)
Tortella tortuosa (Hedw.) Limpr. (BUF, RM)
Tortula caninervis (Mitt.) Broth. (BUF, NY, RM)
Tortula inermis (Brid.) Mont. (Porter 1935)
Tortula mucronifolia Schwaegr. (BUF, NY, RM)
Tortula norvegica (Web.) Wahlenb. *ex* Lindb. (BUF, RM)
Tortula papillosissima (Copp.) Broth. (BUF, RM)
Tortula ruralis (Hedw.) Gaertn., Meyer & Scherb. (BUF, RM)
Trichostomopsis australasiae (Grev. & Hook.) Robins. (BING, BUF)

Pterygynandraceae

Heterocladium dimorphum (Brid.) Schimp. *in* BSG (BUF)
Myurella julacea (Schwaegr.) Schimp. *in* BSG (RM)

Rhytidiaceae

Rhytidium rugosum (Hedw.) Kindb. (WTU)

Seligeriaceae

Blindia acuta (Hedw.) Bruch & Schimp. *in* BSG (COLO, CSU, RM)
Seligeria campylopoda Kindb. *in* Macoun & Kindb. (ALTA, BUF, RM)

Sphagnaceae

Sphagnum angustifolium (C. Jens. *ex* Russ.) C. Jens. *in* Tolf (COLO, RM)
Sphagnum annulatum H. Lindb. *ex* Warnst. (BING, RM)
Sphagnum contortum Schultz (BING)
Sphagnum fimbriatum Wils. *in* Wils. & Hook. f. (COLO, RM)
Sphagnum fuscum (Schimp.) Klinggr. (RM)
Sphagnum platyphyllum (Lindb. *ex* Braithw.) Sull. *ex* Warnst. (RM)
Sphagnum russowii Warnst. (RM)
Sphagnum squarrosum Crome (RM)
Sphagnum subsecundum Nees *in* Sturm (BING)
Sphagnum teres (Schimp.) Aongstr. *in* Hartm. (BING)
Sphagnum warnstorfii Russ. (RM, COLO)

Splachnaceae

Splachnum sphaericum Hedw. (YELLO)
Tayloria acuminata Hornsch. (Crum and Anderson 1981)
Tayloria ligulata (Dicks.) Lindb. (COLO, RM)
Tayloria serrata (Hedw.) Bruch & Schimp. *in* BSG (NY)

Tetraphidaceae

Tetraphis pellucida Hedw. (RM)

Thuidiaceae

Abietinella abietina (Hedw.) Fleisch. (BUF, RM)

Timmiaceae

Timmia austriaca Hedw. (BUF, RM)

Timmia megapolitana Hedw. var. *megapolitana* (NY, RM)
var. *bavarica* (Hessl.) Brid. (BUF, RM)

PROBLEMATIC TAXA

Brachythecium campestre (C. Muell.) Schimp. *in* BSG. Old Faithful, Yellowstone National Park, Smiley, according to Porter (1934, 1935). Porter's citation is apparently not based on a specimen but on Dwight Smiley's checklist. Since this is primarily a taxon of the eastern United States, it should probably be excluded from the state flora. Specimen not seen.

Brachythecium oxycladon (Brid.) Jaeg. This taxon, typical of the eastern United States, is based by Porter (1934, 1935) on a citation by Smiley. No corresponding specimens were seen.

Funaria flavicans Michx. No specimens were seen of this taxon reported by Porter (1935). As it appears to be a species of the eastern region of the United States (Crum and Anderson 1981), it is of doubtful occurrence in Wyoming.

Mnium hornum Hedw. (Porter 1935). This is a taxon of the eastern montane region of North America and the Piedmont (Crum and Anderson 1981) and not likely to occur in Wyoming. No specimen seen.

Platydictya confervoides (Brid.) Crum. Cited by Porter (1935) as a doubtful determination; it cannot be located in the herbaria consulted.

Racomitrium fasciculare (Hedw.) Brid. Porter (1935) did not see a specimen of this species, reported by Nelson (1900). Spence's citation for Teton County (1985) refers to Porter's doubtful citation. No specimens were seen by the present author.

EXCLUDED TAXA

Brachythecium calcareum Kindb. A specimen of Smiley's of *Brachythecium flexicaule*, now *B. calcareum*, from Yellowstone National Park and cited by Porter (1935) was determined as a depauperate specimen of *B. frigidum*.

Brachythecium glareosum (Br.) B. & S. Lake, Yellowstone National Park (Smiley) (Porter 1934, 1935). Specimens of Smiley and other collectors at YELLO were variously *Brachythecium salebrosum*, *B. leibergii*, *B. albicans*, and *B. frigidum*.

Breutelia mohriana (C. Muell.) Broth., Carbon Co. (Porter 1937). Excluded from North America (Anderson et al. 1990).

Brotherella recurvans (Michx.) Fleisch., Lincoln Gulch, Albany County (Aven Nelson 2628). "The material is scanty, and Prof. Holzinger, who identified it, expressed a doubt as to the correctness of the determination" (Porter 1935). The specimen with Holzinger's opinion is at RM.

Bryum canariense Brid. (Porter 1935). This is a species of the West Coast and not likely to occur in Wyoming. The specimen cited by Porter (Nelson 7814) curated at RM and US seems to be *Bryum caespiticium* Hedw.

Encalypta streptocarpa Hedw. (Porter 1930, 1935). Excluded from North America (Anderson et al. 1990).

Gymnostomum calcareum Nees & Hornsch. *in* Nees et al. (Porter 1937. "Washakie Co."). The specimen from WTU of Porter, Sept. 9, 1935, No. 2094, "On limestone boulders in a shady canyon" from the Ten Sleep Canyon in the Big Horn Mts, Washakie, Co., has been determined to be *Gymnostomum aeruginosum* by R. Zander. The specimen in section shows a ventral costal epidermis, two stereid bands, a central strand in the stem. The capsules were young and so rather ovoid.

Homalothecium lutescens (Hedw.) Robins. Based on a citation by Porter (1937) and probably the specimen: Yellowstone National Park Nelson No. 6041 (RM) appears to me to be *Homalothecium aeneum* instead.

Hypnum callichroum Funck. *ex* Brid., Evanston, Uinta County (Aven Nelson 4128, in part: "The identity of this plant is doubtful," Porter 1935; Uinta Co., Porter 1937). The specimen Nelson 4128 appears to be *Hypnum lindbergii*.

Macrocoma sullivantii (C. Muell.) Grout (BUF). This record is due to a labeling error (Vitt 1981; D. Vitt, *in litt.*). in the Orthotrichaceae Boreali—Americanae Exsiccatae Fasciculus III Nos. 21–30. The label issued with this species name, number 30, should be number 27, *Orthotrichum rupestre*. The *Macrocoma* specimen originated in North Carolina, the *Orthotrichum* from Yellowstone National Park (J. A. Christie, *in litt.*).

Meesia triquetra (Richt.) Aongstr. reported by Cooper and Andrus (1994) is *Oncophorus wahlenbergii*.

Orthotrichum speciosum Nees *in* Sturm (Porter 1935). Specimens at YELLO and RM were determinable as *O. laevigatum*.

Orthotrichum pallens Bruch *ex* Brid. var. *parvum* Vent., "Yellowstone National Park"

(Flowers 1973). Excluded from North America (Anderson et al. 1990).

Physcomitrium pyriforme (Hedw.) Hampe, cited by Porter (1937) for Crook Co., is probably a specimen collected by Marion Ownbey from that county (No. 556a, TENN) and determined by Porter as *P. turbinatum*, but which, upon examination, is *P. hookeri.*

Plagiomnium affine (Bland. *ex* Funck) T. Kop. (Porter 1935). Excluded from North America (Anderson et al. 1990).

Plagiothecium cavifolium (Brid.) Iwats. Porter (1935) based this name on a specimen of Elias Nelson (5242), which is *Isopterygiopsis pulchella.*

Sphagnum capillifolium (Ehrh.) Hedw. (Porter 1935). Porter's specimens 1198 and 1199 collected in 1932 identified as *S. capillifolium* had been redetermined by R. Andrus as *S. russowii* (Andrus *in litt.*).

Sphagnum majus (Russ.) C. Jens. (Porter 1935, Crum 1984). Taxa collected from Wyoming and identified as *S. majus* have all been *S. annulatum*, according to Andrus (*in litt.*), who states that the nearest sites would be in British Columbia, central Alberta, and Minnesota.

Sphagnum palustre L. (COLO, RM). This species has been found only along the West Coast by Andrus (*in litt.*).

Sphagnum recurvum P. Beauv. (COLO, RM). Material of this species from the interior of the United States is referable to *S. angustifolium*, according to Andrus (*in litt.*). *Sphagnum recurvum* is an eastern coastal plain species.

Tortula princeps De Not. Reports by Porter from Carbon and Crook counties (1935) were based on Nelson 2818 and 5034 at RM, and a specimen (RM) by Hermann (No. 17844), which were redetermined by R. Zander as *Tortula ruralis.*

Weissia controversa Hedw. (Porter 1935). All citations for this species appear to be based on specimens of Dwight C. Smiley, deposited at YELLO. All 3 specimens seen were *Dicranoweisia crispula.*

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VARIATION IN BITTERBRUSH (*PURSHIA TRIDENTATA* PURSH) CRUDE PROTEIN IN SOUTHWESTERN MONTANA

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ABSTRACT.—The objective of this study was to determine if crude protein varies significantly during late summer and midwinter among stands of bitterbrush (*Purshia tridentata* Pursh) in southwestern Montana. A secondary objective was to determine if leaves, when present, contribute significant additional protein in the region. Nine sites with different environmental conditions and within a radius of 14.5 km were studied. Bitterbrush leaves and leaders collected in August 1990 and 1991 and February 1991 were used for crude protein and leaf-to-leader ratio determinations. Crude protein differed ($P < 0.001$) among sites for both leaves and leaders on individual collection dates. Crude protein in leaves was nearly twice the level found in leaders. Because few leaves were present in February, they increased crude protein in total foliage by only 0.3% over twigs alone. February crude protein levels averaged 6.8% for total foliage, which is below the estimated requirement for wintering deer.

Key words: Purshia tridentata, *bitterbrush, crude protein, winter range, big game nutrition, Montana.*

Protein is one of the most important nutrients for wintering ungulates (Dietz 1972). Welch et al. (1983) estimated that winter crude protein levels of *Purshia tridentata* Pursh (bitterbrush) are not high enough to meet ungulate requirements, but postulated that protein content might vary with populations of bitterbrush. Differences in bitterbrush protein content between sites have been noted (Giunta et al. 1978), although not between local habitat types (Morton 1976). Slausen and Ward (1986) found no difference in crude protein among 3 Colorado accessions in a common garden, but Welch et al. (1983) found differences in a common garden test with plants from a wider geographical area. No differences in nutrient content have been found at varying browse levels of bitterbrush plants (Dietz et al. 1962, Shepherd 1971). Crude protein levels were higher when winter leaves were present (Dietz et al. 1962), but winter leaf presence varies between populations of bitterbrush (Welch et al. 1983).

Our objective was to determine if crude protein varies significantly during late summer and midwinter among stands of bitterbrush in southwestern Montana. Secondarily, we wished to determine if bitterbrush leaves in our region contribute significant additional crude protein quantities when present.

METHODS

Study Sites

Nine study sites were chosen primarily to represent bitterbrush stands from a range of environmental conditions (Table 1). This included burned sites and bitterbrush sites protected from browsing. All study sites were located within a radius of 14.5 km near Butte and Anaconda in southwestern Montana. Long-term climatic records were available for the general study area from the Anaconda weather station at 1700 m elevation. Annual precipitation at Anaconda averages 340 mm, with 47% received between April and July (NOAA 1991).

Vegetation types at all but 3 sites (burn, unburn, and High Rye) were seral stages of the bitterbrush–bluebunch wheatgrass (*Agropyron spicatum* Pursh) habitat type (Mueggler and Stewart 1980). The dominant shrub was bitterbrush, but understory vegetation was regressed (Fraas et al. 1992) on the other 6 sites from the described potential climax composition (Youtie et al. 1988).

The Butte site at Maude S Canyon, near Butte, Montana, was selected because it receives no ungulate browsing. The plant community consisted of bitterbrush, *Centaurea maculosa* Lam. (spotted knapweed), *Ribes cereum* Dougl. (squaw currant), and *Rosa woodsii* Lindl. (Woods rose).

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TABLE 1. Topographic characteristics of the 9 study sites. Data from the last 4 sites were obtained from Guenther (1989).

Site	Elevation (m)	Slope (%)	Aspect (degrees)
Butte	1730	26	234
Cattle exclosure	1830	16	188
Cattle + deer	1820	10	190
Burn	2010	21	220
Unburn	2010	24	180
Powerline	1640	16	85
Willow Creek	1780	31	110
Railroad Gulch	1650	32	115
High Rye	1940	38	120

At Dry Cottonwood Creek in the Deerlodge district of the Deerlodge National Forest, a livestock exclosure with deer-only use was studied and known as the cattle exclosure site. Near the exclosure, a bitterbrush stand was studied and known as the cattle + deer site because it sustained both cattle and mule deer browsing. These 2 sites have a scattered overstory of *Pseudotsuga menziesii* [Mirb.] Franco (Douglas-fir). A high number of native perennial forbs occurred in the understory on these sites.

Two sites were selected to gauge the impacts of burning bitterbrush in southwestern Montana. The 2 sites (burn, unburn) were situated on either side of the burn line on the south flank of Steep Mountain, 8 km northwest of Butte, in the Butte District of the Deerlodge National Forest. The plant community on these 2 sites was a bitterbrush–mountain big sagebrush (*Artemisia tridentata* Nutt. ssp. *vaseyana* [Rydb.] Beetle)–bluebunch wheatgrass association intermediate to the big sagebrush–bluebunch wheatgrass and bitterbrush–bluebunch wheatgrass habitat types of Mueggler and Stewart (1980). The prescribed burn was conducted 3 November 1981 after a year's rest from livestock grazing to increase fuel loads. Livestock use resumed 15 September 1982. When sampled for protein content, bitterbrush on the burned site was significantly lower in canopy cover ($P > 0.01$), flower production ($P > 0.1$), and seed production ($P > 0.1$) than on the unburned site (Fraas et al. 1992).

Four sites were located on the Mount Haggin Wildlife Management Area (MHWMA), owned and managed by Montana Fish, Wildlife, and Parks. The Powerline site was on a slope 50 m above a perennial stream on the northeast edge of the MHWMA big game winter range. The plant community consisted of bitterbrush and spotted knapweed. The Willow Creek site was near the top of a grassy ridge 150 m above Willow Creek. This site supported a relatively large amount of *Elymus cinereus* Scribn. & Merr. (basin wild rye), along with other perennial grasses and bitterbrush. This area was used as winter range by mule deer, elk, and moose. The Railroad Gulch site was also on the deer and elk winter range. This site occupied a midslope position 30 m above an intermittent stream, where the plant community consisted of bitterbrush and spotted knapweed. The High Rye site was 1500 m higher in elevation than the other MHWMA sites and appeared to receive the greatest snowpack. The plant community on the High Rye site was typical of the bitterbrush–rough fescue (*Festuca scabrella* Torrey ex Hook.) habitat type (Mueggler and Stewart 1980) with those species currently dominant. Guenther (1989) found the least amount of big game use at this location among the 4 MHWMA sites. The MHWMA study sites received insignificant levels of livestock grazing.

Sampling and Analysis

Leaves and leaders (current-year stem growth minus leaves) were collected at each study site from 10 randomly selected plants for crude protein analysis on each of the sampling dates. The same plants were sampled to determine leaf-to-leader ratios. Material was collected the 1st week of August prior to or at seed set in 1990 and 1991. This was estimated to be the period of minimum soluble carbohydrate content for bitterbrush plants (Menke and Trlica 1981). Material was also collected on 12 February 1991, when mule deer were concentrated on these sites. Plant material was oven-dried at 60°C for 48 h and weight of dry matter determined. Leaves were separated from leaders and weighed separately to determine leaf-to-leader ratios on a percent dry matter basis. Leaves and leaders were then ground to approximately 1 mm diameter in a grinder (Janke & Kunkel kg, type A10). Kjeldahl (nitrogen) analyses were used to arrive at crude protein contents. Winter crude protein values were calculated with a weighted average of winter leaf and leader protein levels. This allowed comparison with other studies (Dietz et al. 1962, Welch et al. 1983).

Soil samples were obtained at a depth of 15 cm below the surface from a soil pit in each study plot. Because soils at most sites contained a large rock fraction, it was necessary to sample at the relatively shallow depth of 15 cm to standardize sampling. The Montana State University Soil Test Laboratory performed organic matter determinations and total Kjeldahl nitrogen analyses on all non-MHWMA samples. Texture was determined by both the hydrometer and Bouyucous mechanical analysis methods. Soil pH was determined in 1 part soil to 2 parts water extractions. Topographic information was also recorded at each site. Aspect was determined by taking a compass bearing from the major slope. Slope was measured with a clinometer. Elevation was determined from USGS topographic maps. The information from MHWMA sites was derived from Guenther (1989).

A one-way ANOVA, with site as the factor, was conducted for each sampling date and protein source combination (Snedecor and Cochran 1989). This was done with the knowledge that protein sources (leaves or leaders) contained very different levels of crude protein within each sampling date. Site was also the factor in an ANOVA for percent leafiness for the February 1991 sample. The least significant difference (LSD) method ($P < 0.05$) protected by a prior F-test ($P < 0.05$) was used for comparing treatment means (Snedecor and Cochran 1989).

RESULTS AND DISCUSSION

Crude protein levels differed ($P < 0.001$) among sites within each protein source and collection date combination (Fig. 1). Thus, we rejected the hypothesis that crude protein values are equal during August and February among local stands of bitterbrush. Crude protein in the leaves, when averaged over all sites, varied with a 13% to 10% decline from August 1990 to February 1991 and subsequent increase to 15% by August 1991. Crude protein in the leaders for these 3 dates was 7.1%, 6.5%, and 7.2%, respectively, when averaged over all sites. These crude protein levels generally agreed with previous reports for bitterbrush throughout its range (Dietz et al. 1962, Bayoumi and Smith 1976, Morton 1976, Tiedemann 1983, Welch et al. 1983).

Protein levels also differed ($P < 0.001$) among the 3 collection dates (Fig. 1). When all sites were pooled, August leaf protein increased 11% between years ($P < 0.05$) and February leaf protein decreased 21% from August levels ($P < 0.001$). Leader crude protein did not vary significantly between years but was higher in August 1991 than during the previous February ($P < 0.05$).

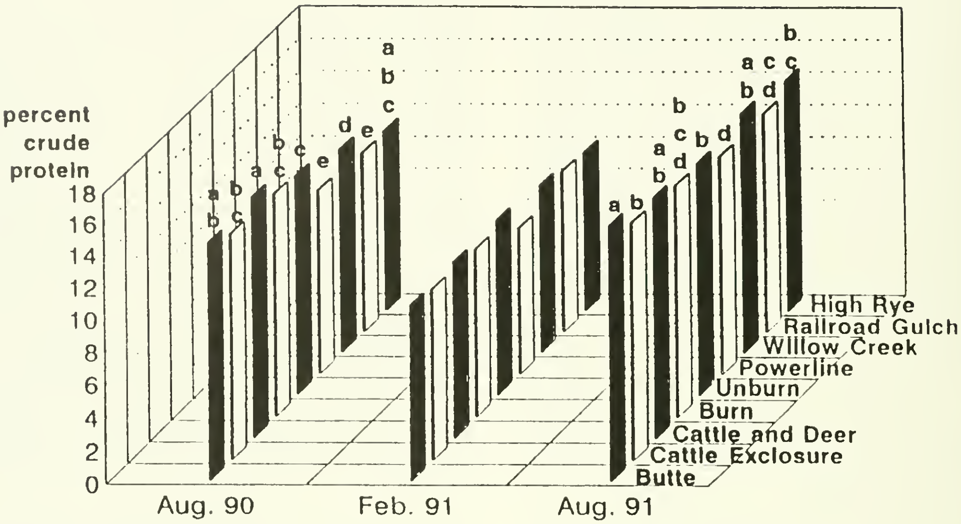
The unbrowsed Butte site rated highest in crude protein (Fig. 1) for 3 of the 6 measurements, although none was significantly higher than the next lower site. When the Butte site was compared to the aggregated crude protein levels of the other 8 sites, it was significantly ($P < 0.05$) higher for both leaves and leaders in August 1990, but did not differ from browsed sites in February or August 1991. Thus, it does not appear that browsing affects crude protein levels.

Protein values for the 4 MHWMA sites were lower for August 1990 leaves ($P < 0.07$) and leaders ($P < 0.01$) than for other sites and collectively rated lowest for 4 of the 6 measurements. These site differences were not expected from Morton's (1976) work, but were supported by that of Giunta et al. (1978) and Welch et al. (1983).

Bitterbrush crude protein levels on the deer + cattle site were 1% higher ($P < 0.05$) than on the adjacent cattle exclosure site for August 1990 leaves (Fig. 1). Other protein levels did not differ significantly between these 2 sites. Although a difference in use might thus seem to affect protein levels on these sites, the unbrowsed Butte site had higher protein levels than browsed sites in August 1990 ($P < 0.05$) and no difference in February or August 1991.

Related to these site and possible population (Alderfer 1977) differences are soil differences. Soil samples from shrub interspaces (Table 2) contained 49% more soil nitrogen at the Butte site than at the burn and unburn sites and 78% more than at the cattle exclosure and deer + cattle sites. Bayoumi and Smith (1976) found a positive response of bitterbrush protein levels to fertilization with nitrogen, although Tiedemann (1983) found slightly negative to no response to fertilization. However, most desert shrubs accumulate nutrients under their canopies, and the surrounding interspaces have low nutrient content (Garcia-Moya and McKell 1970, Tiedemann and Klemmedson 1973), conditions that we did not sample.

Leaves



Leaders

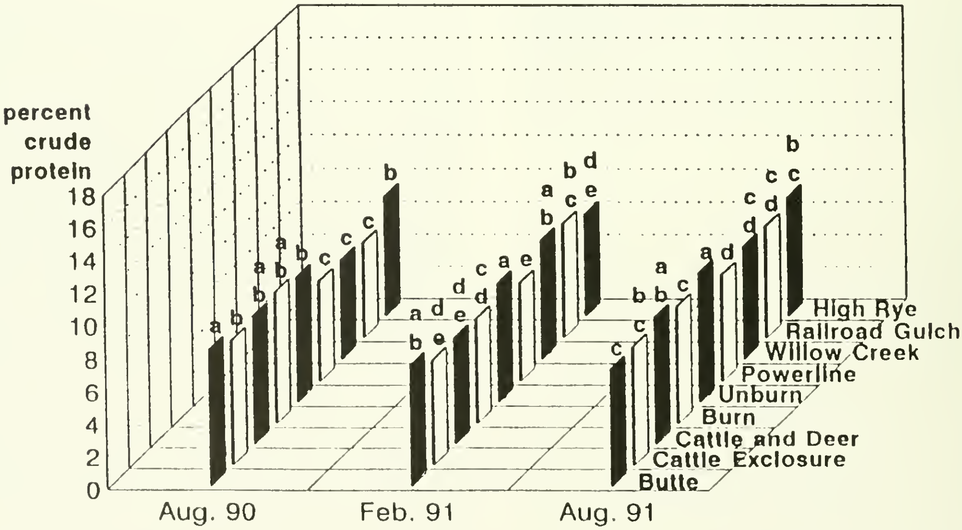


Fig. 1. Average percent crude protein in bitterbrush leaves and leaders found in August 1990, February 1991, and August 1991. Protein values within each protein source and collection date with similar lowercase letters are not significantly different (LSD, $P > 0.05$). Insufficient leaf material was available for statistical analysis in February 1991.

TABLE 2. Soil characteristics for study areas, including pH, organic matter (OM), total Kjeldahl nitrogen (N), percent sand, silt, and clay, and textural class. Soil nitrogen was sampled at only 5 sites. Data from the last 4 sites were obtained from Guenther (1989).

Site	pH	OM (%)	N (%)	Sand (%)	Silt (%)	Clay (%)	Textural class
Butte	5.6	2.6	0.11	63	24	13	sandy loam
Cattle exclosure	5.7	1.0	0.06	80	12	8	loamy sand
Cattle + deer	5.7	1.0	0.06	80	12	8	loamy sand
Burn	6.3	1.1	0.07	67	23	10	sandy loam
Unburn	6.3	1.1	0.07	67	23	10	sandy loam
Powerline	5.8	1.4	—	65	15	20	sandy loam
Willow Creek	5.2	3.6	—	65	18	17	sandy loam
Railroad Gulch	5.7	1.0	—	72	18	10	sandy loam
High Rye	6.7	2.8	—	69	15	16	sandy loam

Protein levels at our study sites were therefore not necessarily related to soil nitrogen levels.

Although most leaves had fallen by February, all sites contained plants that had retained some leaves at that time. Bitterbrush phenology seems to vary more by season and climate than by ecotype (Shaw and Monsen 1983). Most leaves are deciduous, dropping in response to moisture stress in late summer or fall (Shaw and Monsen 1983), but some small leaves overwinter on some populations (Alderfer 1977). Dietz et al. (1962) alluded to the high protein level of leaves in winter but did not quantify those levels. Welch et al. (1983) reported that winter leafiness (presumably, weight of leaves compared with weight of stems) of plants from Idaho, Colorado, Utah, and California ranged from 5.9% to 15.5%, while combined leaf and leader crude protein ranged from 5.9% to 7.9%. These ranges are similar to values found for these Montana sites: leafiness (percent weight of leaves per weight of stems) of 1.5% to 15.8% and combined crude protein of 6.1% to 7.6% (Table 3). Because so few leaves were present in February (Table 3), crude protein in total foliage increased by only 0.3% over twigs alone for all sites.

Although we concluded that leaves contain significantly more crude protein than leaders on our study sites, leaf scarcity during winter in our region prevents total (leaf and leader) crude protein from meeting deer requirements (Welch et al. 1983). The February crude protein levels for total foliage averaged 6.8% across sites, which were below the estimated necessary threshold of 8.9% for wintering deer (Welch et al. 1983). However, September through November protein levels might have been higher, as many plants retained leaves through that period.

Guenther (1989) reported that deer pellets from the MHWMA sites contained large amounts of Rocky Mountain juniper (*Juniperus scopulorum* Sarg.) and Oregon grape (*Berberis repens* Lindl.). Protein values for small winter samples of Oregon grape and juniper from the Willow Creek site were 8.4% and 6.9%, respectively. These values are below those reported by Welch et al. (1983) and, like bitterbrush, are also below what they considered to be the necessary threshold of 8.9% crude protein for wintering deer. Hamlin and Mackie (1989) suggested that mule deer have more need for high-quality forage in the fall, while building energy reserves, than in the winter. Bitterbrush in southwestern Montana may supply this needed level of nutrients in the fall, as we observed delayed leaf-fall on wind-protected bitterbrush plants in late November 1990, but we did not sample plants at that time.

Restoration efforts for ungulate winter ranges capable of maintaining bitterbrush may benefit through consideration of our results. We have found that bitterbrush populations of even a localized ecotype, such as we studied, should not be expected to attain the same levels of crude protein over different environmental conditions that will vary between sites. Revegetation of bitterbrush ranges will involve consideration for obtaining the best possible plant materials. Our evidence indicates that plant characteristics, other than protein content, should likely be of primary concern as protein can be expected to vary by site conditions regardless of plant material. However, it appears that consideration should be made of bitterbrush genotypes that maintain a high percentage of leaves into the winter. These genotypes may provide a higher level of crude protein that is desirable for wintering ungulates.

TABLE 3. Winter crude protein content (percent) of bitterbrush leaves and leaders combined and percent leafiness (percent weight of leaves per weight of stems) for study sites sampled February 1991. Column entries with similar letters are not significantly different (LSD, $P < 0.05$).

Site	Crude protein (%)	Leafiness (%)
Butte	7.6^{a}	13.6^{ab}
Cattle exclosure	6.4^{cd}	6.5^{d}
Cattle + deer	6.6^{c}	9.9^{c}
Burn	6.7^{bc}	9.6^{cd}
Unburn	7.6^{a}	10.5^{bc}
Powerline	6.1^{d}	8.5^{cd}
Willow Creek	7.1^{ab}	8.1^{cd}
Railroad Gulch	7.2^{a}	15.8^{a}
High Rye	6.1^{d}	1.5^{e}

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DAM-FORMING CACTI AND NITROGEN ENRICHMENT IN A PIÑON-JUNIPER WOODLAND IN NORTHWESTERN ARIZONA

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ABSTRACT.—In a piñon-juniper woodland in northwestern Arizona, connected basal cladodes of a prickly pear cactus (*Opuntia littoralis* var. *martiniana*) form check dams that cause deposition of N-rich detritus in interspaces otherwise lacking litter. Seventy-eight percent of connected basal cladodes measured in transects grew at an angle (with respect to the slope contour) ≤ 45°—an orientation facilitating deposition of flood-borne debris.

Soil total N was significantly greater ($P < 0.01$) and organic C was greater, but not significantly, above cactus dams compared to below cactus dams. Soil total N and organic C both above and below cactus dams were significantly greater ($P = 0.0001$) compared to adjacent interspaces. Soil total N and organic C above cactus dams were equal to areas beneath canopies (tree and shrub combined). Net NO_3^- (0–5 cm depth) above cactus dams was significantly greater ($P = 0.0001$) than below cactus dams, at interspaces, and beneath canopies. Net NH_4^+ (0–5 cm soil depth) above cactus dams was significantly greater ($P < 0.01$) than below cactus dams and interspaces, and was greater (but not significantly) than beneath canopies. At 5–10 cm soil depth, differences in net NH_4^+ and net NO_3^- between sampling locations were not significant except for the difference in net NO_3^- above and below cactus dams ($P < 0.05$). The litter layer above cactus dams had twice as much total N ($P < 0.01$) as the litter layer beneath canopies (tree and shrub combined); differences in net mineralized N were not significant between litter layers. Over the course of a single rainy season, detritus depth behind cactus dams increased up to 23 cm, with a mean increase of 4.3 cm ($s_{\bar{x}} = 0.625$, $P = 0.0001$).

Key words: prickly pear cactus, nitrogen enrichment, growth habit, soil characteristics, check dams, detritus, runoff, bulk density, total nitrogen, organic carbon, mineral nitrogen, piñon-juniper woodlands, islands of fertility.

The growth habit of *Opuntia littoralis* var. *martiniana* (L. Benson) L. Benson consists of connected basal cladodes growing across woodland slopes roughly along the contour. Cladodes in contact with the ground sprout adventitious roots and become anchored. Sequentially anchored cladodes function as check dams during runoff events, causing deposition of flood-borne detritus including surface soil, animal feces, and litter of piñon pines, juniper, and oak.

Piñon-juniper woodlands occupy at least 17 × 10^6 ha in the western U.S., with widespread distribution in Colorado, New Mexico, Arizona, eastern California, Nevada, and Utah (West 1988). These woodlands fall between mesic conditions that support closed-forest canopies and arid conditions in which plants are widely spaced. Compared with forests of wetter environments, piñon-juniper woodlands have low biomass, leaf area, and primary productivity (Grier et al. 1992). Woodland structure varies but can generally be described as single trees and shrubs and clumps of trees and shrubs surrounded by a network of interspaces (Lanner 1981). Litter occurs in patches due to the noncontiguous canopy cover, and soil N distribution corresponds to litter and canopy distribution (DeBano and Klopatek 1987, Tiedemann 1987). In mixed-species stands, patches may be mosaics of different litter components.

Interspace and canopy area soils usually differ in characteristics such as concentrations of nutrients, pH, bulk density, soil water, and in numbers and species of resident microorganisms and microarthropods (Everett and Sharrow 1985, Klopatek 1987, Klopatek and Klopatek 1987), although there are exceptions to this generalization (DeBano et al. 1987). Soil organic matter and nutrients are concentrated near the soil surface (West and Klemmedson 1978, Lyons and Gifford 1980, DeBano and Klopatek 1987), and runoff from storms can carry considerable amounts of detritus rich in organic matter and N (Fletcher et al. 1978).

Objectives of this study were (1) to characterize the angle of growth (relative to slope contour) of connected basal cladodes of *Opuntia littoralis* var. *martiniana*, (2) to compare litter and soil properties above and below cactus

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TABLE 1. Sites of measurement of angle (relative to the slope contour) of connected basal cladodes. (Samples for soil comparisons were taken only in the Hualapai Mountains [see Table 2].)

Location	Transect length (m)	Soil parent material	Elevation (m)	Aspect	Slope (%)	Piñon pine cover (%)
Cerbat Mountains[a]	401	granite	1930	S-SSE	10–25	10–30
Hualapai Mountains[b]	110	granite	1524	N	15–45	30–40
Music Mountains[c]	302	vesicular basalt	1712	E	30	40–70

[a] 27 km NW of Kingman, AZ (lat.35°27′, long.114°09′; T24NR18WS23nw).
[b] 12 km SE of Kingman, AZ (lat.35°08′, long.113°55′; T20NR16WS1sw).
[c] 53 km NE of Kingman, AZ (lat.35°41′, long.113°49′; T27NR36WS36ne).

dams, and (3) to compare litter and soil properties above and below cactus dams with interspaces and areas beneath canopies.

METHODS

Two distinct physiographic provinces come together in northwestern Arizona: southeast, west, and north of Kingman, Arizona, is the Basin and Range Province, characterized by north-trending fault-block mountain ranges separated by broad desert valleys; the Colorado Plateau lies to the east. This area is the interface of 3 deserts as well as a physiographic interface. North of Kingman is the Great Basin Desert, west is the Mojave Desert, and southwest is the Sonoran Desert. The climate of northwestern Arizona is semiarid (Sellers and Hill 1974). Precipitation is bimodal, occurring mostly in winter and summer months, with more rainfall during winter than summer. Summer rain sometimes occurs as intense thundershowers (Sellers and Hill 1974).

We first observed dam-forming cacti in the Hualapai Mountains (rising to over 2438 m, 12 km southeast of Kingman, Arizona) in the course of data collection for studies of piñon-juniper woodland productivity. We subsequently visited 2 nearby ranges (the Cerbat Mountains [over 2133 m at highest point] 29 km northwest of Kingman, and the Music Mountains [over 2011 m] 53 km northeast of Kingman) and found dam-forming cacti in these locations. To characterize the angle of growth of connected basal cladodes of prickly pear cacti (our 1st objective), we took angle measurements in July 1991 on all cacti intercepting straight-line transects in the 3 mountain ranges (Table 1). Starting points of line transects were randomly located, and direction of transects was along random azimuths. A total of 233 angle measurements were recorded. Sequentially connected

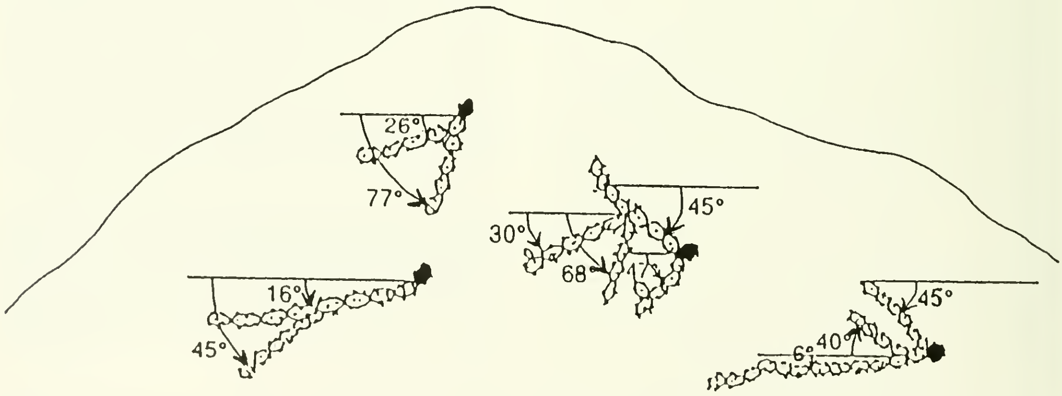

Fig. 1. Measurement of angle of growth of connected basal cladodes with respect to the slope contour. Point of origin indicated by solid cladode.

basal cladodes with series ranging from 0.4 m to 2.5 m in length were measured with an engineer's adjustable triangle as shown in Figure 1: a direction of growth parallel to slope contour was 0° while a direction of growth perpendicular to slope contour, either upslope or downslope, was 90°.

TABLE 2. Characteristics of litter and soil sampling site in a piñon-juniper woodland in the Hualapai Mountains of northwestern Arizona. Records (1967–1991) of licensed livestock grazing show year-round grazing of cattle and horses with year-to-year variation in season of heaviest use and in number of animals (USDA BLM 1991).

Elevation: 1524 m (5000 ft)
% slope: 20-40
Aspect: north
Soil parent material: granite
Soil texture: sandy-loam
Soil classification[a]: Barkerville Series\
loamy, mixed, mesic, shallow\
Udorthentic haplustolls

Other soil characteristics[b]:
A1 horizon 10 cm deep, 39% coarse frag.
pH surface soil interspace—6.5
pH surface soil under canopy—8.0
non-calcareous throughout

Species and % cover[c]:		
Pinus monophylla subsp. *fallax*	36.0%	$s_{\bar{x}}$ 5.7
Juniperus osteosperma	4.0%	$s_{\bar{x}}$ 1.6
Quercus turbinella	30.0%	$s_{\bar{x}}$ 6.2
Yucca bacatta	4.0%	$s_{\bar{x}}$ 1.1
Opuntia littoralis var. *martiniana*	1.9%	$s_{\bar{x}}$ 1.1
Rhus trilobata	0.7%	$s_{\bar{x}}$ 0.4
Ceanothus greggii	0.4%	$s_{\bar{x}}$ 0.2
Canotia holocantha	0.3%	$s_{\bar{x}}$ 0.3
Bouteloua gracilis	2.9%	$s_{\bar{x}}$ 1.3
Gutierrizia sarothrae	<1%	

[a] Richmond and Richardson (1974).

[b] Unpublished data, this study.

[c] Two methods were used to estimate cover. For all species, estimates were made on eighteen 2-m^2 plots according to coverage class ratings (Daubenmire 1968). Tree and shrub cover were estimated on 12 permanent 25-m line transects as % Cover = [(25*3.14/Transect Length)] [Sum of crown diameters] (Meeuwig and Budy 1981). Values reported here for trees and shrubs are averages of both methods, and standard errors are from pooled variances.

Soil and Litter Sampling

SITE DESCRIPTION.—We restricted litter and soil sampling to 1 of the 3 transect locations (the Hualapai Mountains, 12 km southeast of Kingman [Table 2, Fig. 2]), to minimize confounding factors such as different soil types, site histories, and land-management practices. About 40% of the study site is open interspaces (combined data [unpublished] from eighteen 2 × 2-m plots using Daubenmire's [1968] coverage classes, and from 12 permanently marked 25-m-long line transects using methods described in Meeuwig and Budy [1981]). Interspaces are mostly bare soil and rock surface, with 3% grass cover (mostly *Bouteloua gracilis* [H.B.K.] Lag. ex Steudel and *B. curtipendula* [Michx.] Torr.) and traces of litter, herbs, and cryptogams. Shrubs, mostly scrub oak (*Quercus turbinella* Greene), cover about 30% of the study area. Piñon pines (*Pinus monophylla* var. *fallax* [Little] Silba) cover about 36% of the area and *Juniperus osteosperma* (Torr.) Little about 4%. The added cover of vegetation components is greater than total vegetation cover due to the presence of different vertical layers of shrub and tree canopies and aggregation of vegetation in clumps. Trees ranged in age from seedlings to about 260 yr (estimated from annual ring counts of cores [unpublished data]). Age estimates are approximate due to occurrence of false rings in wood of piñon pines and junipers.

Size range of soil surface patches covered by cacti and associated litter accumulations was estimated by measuring every cactus dam on a 25 × 25-m plot. We recorded length, width, and circumference for each cactus dam and associated litter accumulation (32 total). The area of soil surface covered by cactus dams and litter was calculated as the area of a circle plus 1/2 the difference between the area of a rectangle and a circle.

SOIL AND LITTER SAMPLING APPROACH.—Sampling was stratified by woodland microhabitats: above cactus dams, below cactus dams, interspaces, and beneath canopies. We took paired samples 10.2 cm above (litter present) and below (little to no litter present) cactus axes to compare soil properties above and below cactus dams. We took additional samples from bare interspaces and from areas beneath tree and shrub canopies to compare these areas with the areas above and below cactus dam. Interspaces were considered to lie beyond the influence of canopies and associated litter and beyond the influence of cactus dams and associated litter. Vegetation and litter were scant to absent in interspaces. Beneath tree and shrub canopy, sampling included piñon pines, scrub oaks, junipers, and occasionally mixed-species canopies roughly in proportion to the presence of these components (as estimated by percent canopy cover) on the site (Table 2). The sampling location beneath canopies was at 2/3 canopy radius out from the stem or clump center. Litter of *Yucca baccata*

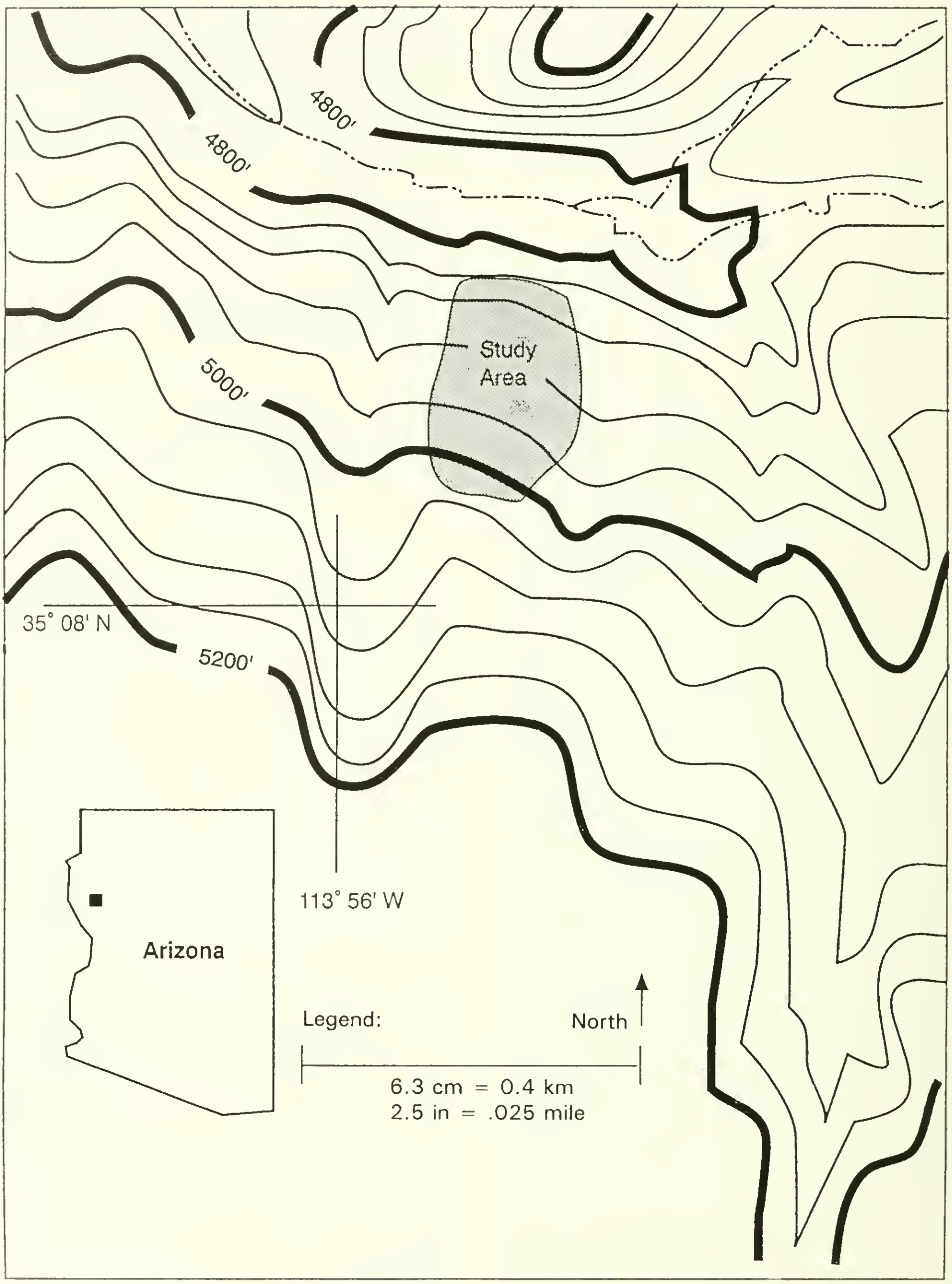
4800'
4800'
Study Area
5000'
35° 08' N
5200'
113° 56' W
Arizona
Legend:
North
6.3 cm = 0.4 km
2.5 in = .025 mile

Fig. 2. Soil and litter sampling area in the Hualapai Mountains of northwestern Arizona. The contour interval is 12.2 m (40 ft). Enlarged from U.S. Geological Survey, Rattlesnake Hill, Arizona Quadrangle.

Torr. and a few other species was occasionally (though rarely) present in litter samples along with litter of the dominant species. With the exception of bulk density samples, soil and litter samples were composited within microhabitat strata by combining equal numbers of equal-sized individual samples. Compositing followed guidelines in Peterson and Calvin (1986) and was suitable for the present study since we were not examining variation within microhabitats. As pointed out by Crépin and Johnson (1993), composite sampling can be used in conjunction with stratification; i.e., the landscape can be divided into meaningful units and good averages of soil properties obtained by compositing samples within each unit. All soil and litter sampling was conducted in July 1991.

BULK DENSITY.—Bulk density was determined by the excavation method (Blake and Hartge 1986). Twenty-two paired samples were taken 10.2 cm above and below cactus axes, 10 samples were taken from interspaces, and 10 were taken from beneath tree and shrub canopies. Soil was excavated with a bulb planter (diameter 5.5 cm at cutting edge), creating a hole 7 cm deep. A thin, tough plastic bag was placed in the hole, filled with water, and then emptied into a graduated cylinder to determine hole volume. Extracted soil was dried at 105° C and weighed, resulting in a weight-to-volume measurement.

TOTAL N, TOTAL ORGANIC C, AND SOIL TEXTURE.—Thirty pairs of soil cores (mineral soil surface to 7 cm deep) were extracted with a bulb planter (diameter 5.5 cm at the cutting edge) adjacent to cactus axes (10.2 cm above and below cactus axes), 30 from beneath canopies, and 30 from interspaces. Samples were taken near each of the 6 satellite plots established for the net mineralization study (see below). Litter (all litter from surface to mineral soil) was retained for determination of total N. Samples were air-dried and stored in paper wrappers. Soil samples originally taken for determining bulk density (see above) were added to these soil samples for a total of 51 samples from each side of cactus dams, 40 samples from beneath canopies, and 40 from interspaces. One of the 22 paired bulk density samples was lost and could not be included.

Samples were combined to create composites: above cactus dams 51 samples of soil were composited to make 3 samples of soil, and 30 samples of litter were combined to make 3 litter samples. Below cactus dams (no litter present) 51 samples of soil were composited to make 3 soil samples. Beneath canopies 40 soil samples were composited to make 3 samples of soil, and 30 litter samples were composited to make 3 litter samples. From interspace areas (no litter present) 40 samples were composited to make 3 samples of soil. Analysis was by Utah State University Soils Testing Lab following the Kjeldahl method (Bremner and Mulvaney 1982) to determine percent total N, the Walkley-Black method (Nelson and Sommers 1982) for percent organic C, and methods described by Gee and Bauder (1986) for particle-size analysis.

NET MINERALIZED N.—The total amount of N liberated from organic matter is "gross mineralization"; the quantity remaining after microbial immobilization is "net mineralization" (Carlyle 1986). Net mineral N, the N available for plant uptake, is an index of soil fertility. To compare soil N fertility among woodland sites, net mineral N was assessed by laboratory aerobic incubations (Binkley and Vitousek 1989).

Seven permanent plots were created on the study site, the 1st plot serving as a central point from which 6 satellite plots were created, each 32 m from the central point at 60° intervals beginning with a random azimuth. Because of topography, 1 plot was relocated 32 m from the center of a satellite plot. From each plot center 8 cacti (0.5 to 5 m from center) were selected at 45° intervals beginning with a random azimuth, for a total sample of 56 cacti.

Paired soil samples were taken 10.2 cm from cactus axes on all 7 permanent plots beginning from the easternmost cactus and moving clockwise. Samples were composited combining 4 individual samples into 1 composite sample. Compositing and field processing (see below) were performed immediately upon the extraction of 4 cores. For example, on the 1st plot 4 cores 10.2 cm above cactus axes in the 90°–270° hemisphere of the plot were taken, composited, and field processed before the next 4 cores were drawn. This ensured processing fresh soil. Fourteen composite sample pairs were prepared.

At approximately midpoints of the six 32-m lines creating satellite plots, 2 samples were taken beneath canopies (piñon pines sampled most heavily followed by scrub oak, mixed-species canopies, and juniper) and 2 from interspaces. Composites of 4 individual samples were prepared and field processing completed immediately as each set of 4 cores was drawn. Three composite samples were prepared.

Samples were taken with a 2-cm-diameter soil corer to a depth of 10 cm. Preparation of samples for analysis followed methods outlined in Vitousek et al. (1982): In the field cores were divided into 3 components (litter layer, top 5 cm of mineral soil, and mineral soil between 5 and 10 cm soil depth) and composited. Composite soil samples were sieved through a 2-

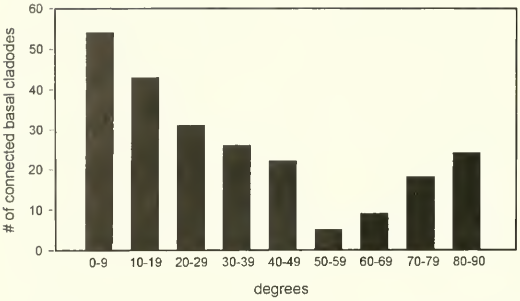

Fig. 3. Angle of growth of connected basal cladodes with respect to slope contour. Zero degrees is a direction of growth parallel to the slope contour; 90 degrees is a direction of growth perpendicular to the slope.

TABLE 3. Size distribution of cactus dams and associated litter accumulations on a 25 × 25-m plot. The area measured was the soil surface covered by cactus dams and associated litter.

Size class (m^2)	Number of cactus dams
0.05	1
0.1–1.0	16
1.1–2.0	6
2.1–3.0	6
3.1–4.0	2
10.30	1

mm screen; litter was not sieved. Subsamples were sealed in bags for determination of moisture content, while a 2nd subsample of approximately 10 g was placed in 100 ml 1 N KCl adjusted with HCl to pH 2.5 with phenylmercuric acetate (PMA) added as a preservative. Solutions were refrigerated, transported to the laboratory, mixed frequently for 4 d, then allowed to settle for 48 h. After settling, the solution was removed with a pipette, and NH_4^+ and NO_3^- were determined at Bilby Research Facility at Northern Arizona University using methods described by Keeney and Nelson (1982).

The remainder of composited field samples (after removal of the above 2 subsamples) was transported to the laboratory and incubated aerobically following procedures in Vitousek et al. (1982): Soils were wetted to approximately field moisture capacity (assessed visually), placed in plastic-covered cups, each of which had a small air hole, and kept in a dark, moist chamber at a constant temperature of 22° C. During an 8-wk incubation period, samples received distilled water (applied as a fine mist to the surface with no mixing) as needed to maintain an approximately constant moisture content. So as not to disturb incubating samples, moisture content was assessed by visible soil color easily observable through the clear plastic incubation cups.

At the end of 8 wk, subsamples (approximately 10 g) of incubated samples were taken for determination of moisture content, and subsamples of approximately 10 g were placed in the KCl solution described above. These solutions were shipped to the soils testing laboratory at Utah State University for determination of NH_4^+ and NO_3^- (U.S. EPA 1983).

CHANGE IN DEPOSIT DEPTH.—Depth of deposits above cactus dams (i.e., above connected basal cladodes) was measured before (July) and after (September) the rainy season of 1991 on 6 of the 7 plots designated for net mineralization sampling (see above). Two sampling points could not be relocated at the end of the rainy season, making a total sample size of 46 cactus dams (i.e., 6 plots, 8 cacti per plot, minus 2). Depth was measured from base to top of deposits in the area of greatest accumulation.

Statistical Analysis

A heterogeneity chi-square analysis followed by a chi-square analysis (Zar 1984) was performed with the 3 data sets of angle of cactus growth from the 3 mountain ranges.

SOIL AND LITTER ANALYSES.—Tests of normality were performed for each data set (above cactus dams, below cactus dams, interspaces, and beneath canopies) of each soil and litter characteristic sampled. A paired *t* test ($\propto = 0.05$) was used to compare means of soil characteristics above and below cactus dams, and to compare the depth of deposits at cactus dams before and after the rainy season. An analysis of variance *F*-test ($\propto = 0.05$) for unbalanced sample sizes (the GLM procedure in SAS software [SAS 1985]) was used to compare sample means of soil above and below cactus dams with beneath canopy and interspace sample means. Plots of residuals were generated to assess equality of variance. Significant differences between means were separated and ranked using a multiple comparison method

TABLE 4. Results of paired *t* tests comparing sample means of soil characteristics above and below cactus dams, and comparing depth of detritus above cactus dams between early July and mid-September. A minus B refers to the value above cactus dams minus the value below.

Attribute	*N*	Paired *t*-test statistics Mean difference A minus B	$s_{\bar{x}}$	*t*	*P*
Bulk density (g/ml) (natural log) 0–7 cm depth	22	–0.222	0.117	1.901	0.0711
Total N (%) 0–7 cm depth	3	0.043	0.003	13.000	0.0059
Organic C (%) 0–7 cm depth	3	0.933	0.231	4.035	0.0563
Net mineralized N (ug/g)					
0–5 cm depth NH_4^+	14	9.621	2.353	4.088	0.0013
0–5 cm depth NO_3^-	14	41.979	5.398	7.776	0.0001
5–10 cm depth NH_4^+	12	2.050	2.063	0.993	0.3418
5–10 cm depth NO_3^-	12	7.550	2.672	2.826	0.0165
Change in depth (cm) of detritus above cactus dams (natural log) 0–7 cm depth	46	1.240[a]	0.124	10.038	0.0001

[a] Mean difference of September detritus depth minus July detritus depth.

(REGWF) cited as being compatible with the overall analysis of variance *F*-test (SAS 1985). A *t* test (∝ = 0.05) was used to compare sample means of total N and net mineralized N from the litter above cactus dams with the litter layer beneath woodland canopies.

RESULTS

The pattern of angle of connected basal cladodes with respect to slope contour was similar in the 3 mountain ranges sampled; data were pooled based on results of a heterogeneity chi-square analysis. Analysis of pooled data ($\chi^2 = 85.4$, $P < 0.001$) indicated that orientation of connected basal cladodes of *Opuntia littoralis* var. *martiniana* was nonrandom: growth was most frequently parallel to the woodland slope contour (Fig. 3). The size range of cactus dams and associated litter on a 25 × 25-m plot at the Hualapai Mountains study area is given in Table 3.

SOIL AND LITTER ANALYSES.—The null hypothesis for normality was not rejected for most of the data sets; however, total N data were nonnormal and were not normally distributed when transformed with standard transformations. Therefore, results of total N analyses should be interpreted with caution. Residual plots indicated equality of variance assumptions were reasonable.

Bulk density above and below cactus dams was not significantly different at $P = 0.05$ (Table 4). Bulk density was significantly lower ($P = 0.0001$) in soil deposits above cactus dams, below cactus dams, and beneath tree canopies, compared to soil from interspaces (Table 5, Fig. 4). Soil above and below cactus dams was also lower in bulk density than soil beneath tree canopies, although this difference was not significant at $P = 0.05$. There was little difference in soil texture among the 4 microhabitats (Table 5).

Soil total N above cactus dams was greater ($P < 0.01$) than below cactus dams (Table 4). Organic C was not significantly different ($P = 0.05$) above cactus dams compared to below cactus dams. Soil total N and organic C were 2–3 times greater ($P = 0.0001$ in both cases) in soil above and below cactus dams than in interspace soil (Table 5, Fig. 4). Soil total N and

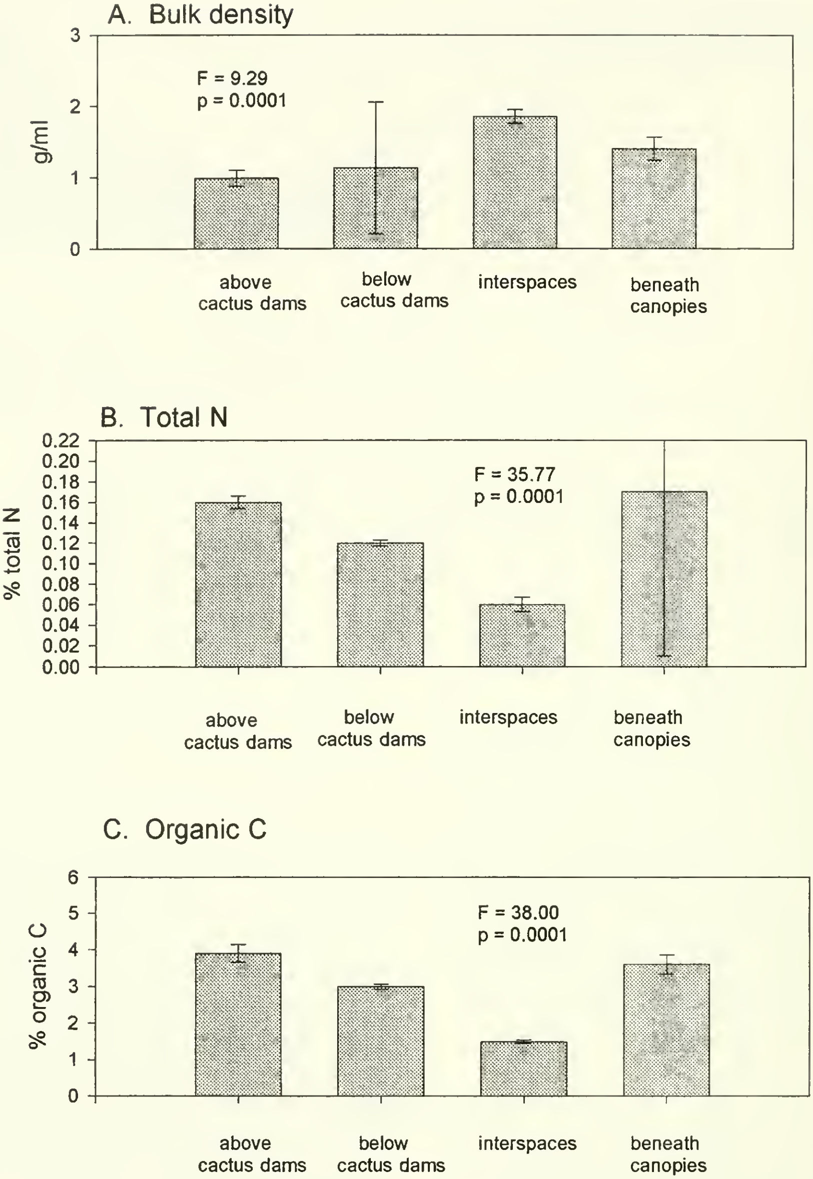

Fig. 4. Comparisons of soil characteristics above cactus dams, below cactus dams, beneath canopies (tree and shrub combined), and in bare interspaces.

organic C above cactus dams were equal to areas beneath canopies. Below cactus dams, soil total N was significantly lower than beneath canopies, and organic C was not significantly different compared to beneath canopies. While soil organic C and soil total N differed among woodland locations, the C:N ratio was similar between locations (Table 5).

Net mineral NH_4^+ and NO_3^- at 0–5 cm depth were significantly greater (P = 0.001 and P = 0.0001) above cactus dams compared to below (Table 4). At 5–10 cm depth net mineral NO_3^- was significantly greater (P = 0.0165) above cactus dams compared to below. Net mineral N in soil 0–5 cm deep above cactus dams was over 3 times that in interspace

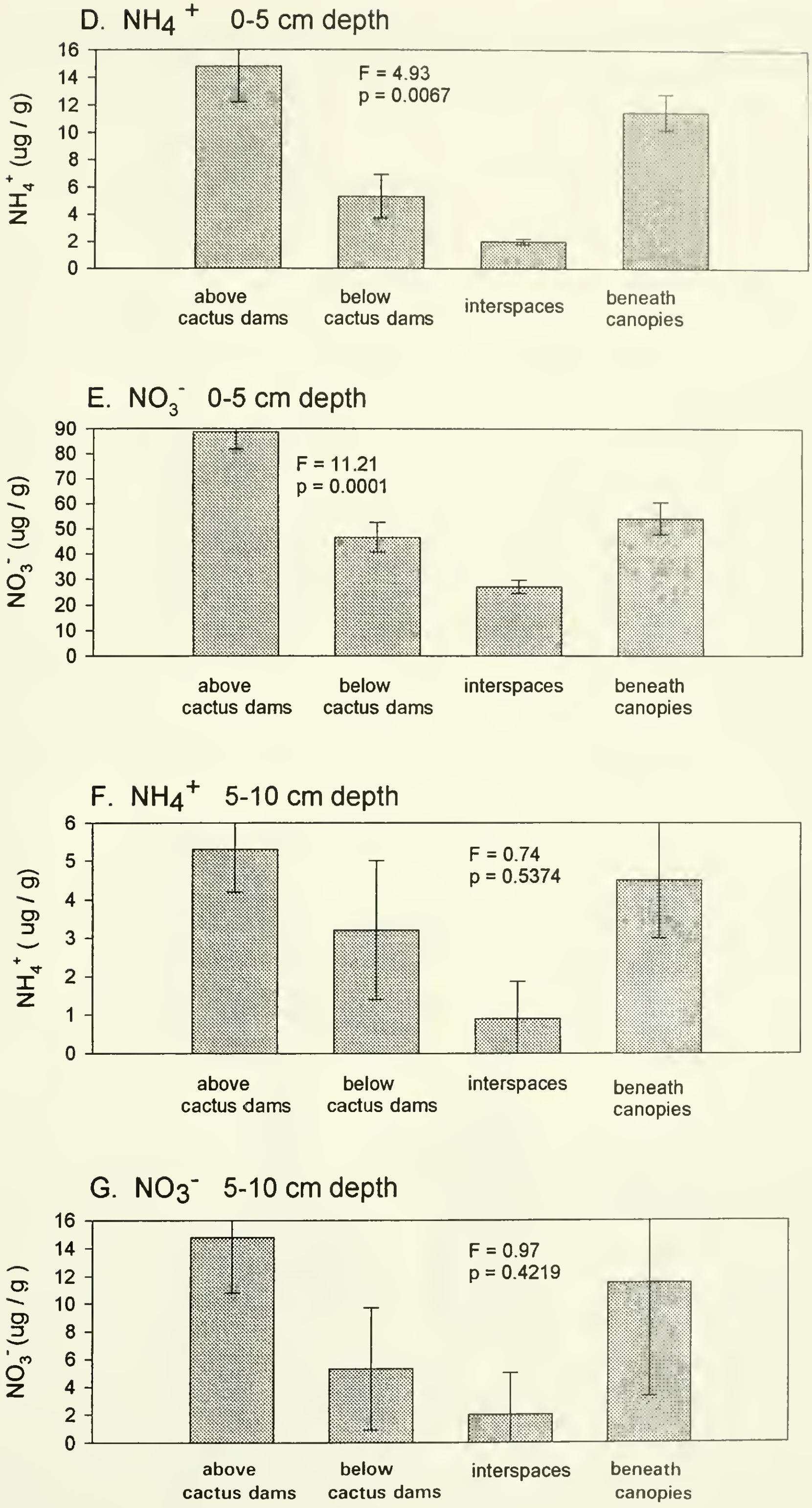

Fig. 4. Continued.

TABLE 5. Comparison of sample means of soil characteristics at 4 woodland microhabitats (above and below cactus dams, interspaces, and beneath canopies) at the Hualapai Mountains site. Superscript letters separate means significantly different at ∝ = 0.05. For texture, s = sand, sl = silt, and cl = clay. Samples are composites except for bulk density. N = sample size and is followed in parentheses by the number of individual samples that were composited.

	Location			
Attribute	Above cactus dams	Below cactus dams	Interspaces	Beneath canopies
Soil texture	sandy loam	sandy loam	sandy loam	sandy loam
% separates	s 65.0	s 63.0	s 63.7	s 62.7
	sl 25.0	sl 26.0	sl 27.6	sl 28.3
	cl 9.0	cl 11.0	cl 8.7	cl 9.0
	$n = 3$ (51)	$n = 3$ (51)	$n = 3$ (40)	$n = 3$ (40)
Bulk density	$\bar{x} = 0.99^{b}$	$\bar{x} = 1.13^{b}$	$\bar{x} = 1.85^{a}$	$\bar{x} = 1.40^{b}$
(g/ml)	± 0.11	± 0.92	± 0.10	± 0.16
	$n = 22$	$n = 22$	$n = 10$	$n = 10$
Total N (%)	$\bar{x} = 0.16^{a}$	$\bar{x} = 0.12^{b}$	$\bar{x} = 0.06^{c}$	$\bar{x} = 0.17^{a}$
0–7 cm depth	± 0.006	± 0.003	± 0.007	± 0.16
	$n = 3$ (51)	$n = 3$ (51)	$n = 3$ (40)	$n = 3$ (40)
Organic C (%)	$\bar{x} = 3.9^{a}$	$\bar{x} = 3.0^{a}$	$\bar{x} = 1.5^{b}$	$\bar{x} = 3.6^{a}$
0–7 cm depth	± 0.24	± 0.07	± 0.04	± 0.26
	$n = 3$ (51)	$n = 3$ (51)	$n = 3$ (40)	$n = 3$ (40)
C:N ratio	24.4	25.0	25.0	21.2
Net mineralized N (ug/g)				
0–5 cm depth				
NH_4^+	$\bar{x} = 14.8^{a}$	$\bar{x} = 5.3^{b}$	$\bar{x} = 2.0^{b}$	$\bar{x} = 11.5^{a}$
	± 2.6	± 1.6	± 0.2	± 1.3
NO_3^-	$\bar{x} = 88.7^{a}$	$\bar{x} = 46.7^{bc}$	$\bar{x} = 27.1^{c}$	$\bar{x} = 54.2^{b}$
	± 6.9	± 5.9	± 2.6	± 6.4
	$n = 14$ (56)	$n = 14$ (56)	$n = 3$ (12)	$n = 3$ (12)
5–10 cm depth				
NH_4^+	$\bar{x} = 5.3$	$\bar{x} = 3.2$	$\bar{x} = 0.9$	$\bar{x} = 4.5$
	± 1.1	± 1.8	± 0.97	± 1.5
NO_3^-	$\bar{x} = 31.6^{a}$	$\bar{x} = 24.0^{b}$	$\bar{x} = 16.6$	$\bar{x} = 30.9$
	± 4.0	± 4.4	± 3.0	± 8.2
	$n = 14$ (56)	$n = 14$ (56)	$n = 3$ (12)	$n = 3$ (12)

soil and almost twice that in soil beneath tree canopies (Table 5, Fig. 4). Net mineral N below cactus dams was greater than in interspaces, but the difference was not statistically significant.

Litter accumulated at cactus dams had total N (0.74%) over twice as high as litter beneath tree and shrub canopies (0.32%) ($t = -8.4$, $P = 0.01$). NH_4^+ and NO_3^- in the litter layer were greater beneath canopies than above cactus dams, but not significantly (Table 6, Fig. 5).

From early July to mid-September, depth of detritus behind cactus dams increased significantly ($P = 0.0001$) from –2 cm to +23 cm, with an average of +4.3 cm ($s_{\bar{x}}$ 0.625; Fig.6).

DISCUSSION

The similarity of soil texture above cactus dams, below cactus dams, beneath tree and shrub canopies, and in interspaces agrees with findings of Schlesinger et al. (1989) that desert soils receiving overland flow and adjacent soils deprived of overland flow were similar in fine material or clay content. The effects of cactus dams and associated litter and detritus deposits on bulk density, total N, organic C, and net mineralized N of nearby soil were expected based on a number of studies in shrub lands and woodlands documenting islands of fertility, i.e., localized areas of nutrient enrichment

TABLE 6. Comparison of total N and net mineralized N in the litter layer beneath canopies with litter accumulations above cactus dams. N = sample size and is followed in parentheses by the number of individual samples that were composited.

	Above cactus dams		Beneath canopies			
Attribute	Mean	$s_{\bar{x}}$	Mean	$s_{\bar{x}}$	t	P
Total N (%)	0.737 n = 3 (30)	0.047	0.320 n = 3 (30)	0.015	–8.4275	0.0095
Net mineralized N (ug/g)						
NH_4^+	60.233 n = 2[a] (12)	15.018	84.550 n = 12[b] (48)	11.250	1.2929	0.2426
NO_3^-	–2.108 n = 2 (12)	6.410	40.050 n = 12 (48)	34.950	1.1865	0.4398

[a] Three composites were prepared; however, initial (before incubation) net mineral N values were not obtained for 1 sample.

[b] Values before incubation were not obtained for 2 of the original 14 composited samples.

(Garcia-Moya and McKell 1970, Tiedemann and Klemmedson 1973, Barth and Klemmedson 1978, Barth 1980, Doescher et al. 1984, Everett et al. 1986, Garner and Steinberger 1989, Schlesinger et al. 1990).

Deposits at cactus dams of *Opuntia littoralis* var. *martiniana* raised soil total N from 0.06% (interspace soil) to 0.16% above connected basal cladodes and to 0.12% below (Table 4). Nitrogen enrichment and soil amelioration associated with deposits at cactus dams may increase cactus productivity. Nobel et al. (1987) observed that while annual aboveground productivity of prickly pear cacti can be high under optimal conditions, cacti productivity is often limited by low levels of soil N (Nobel et al.

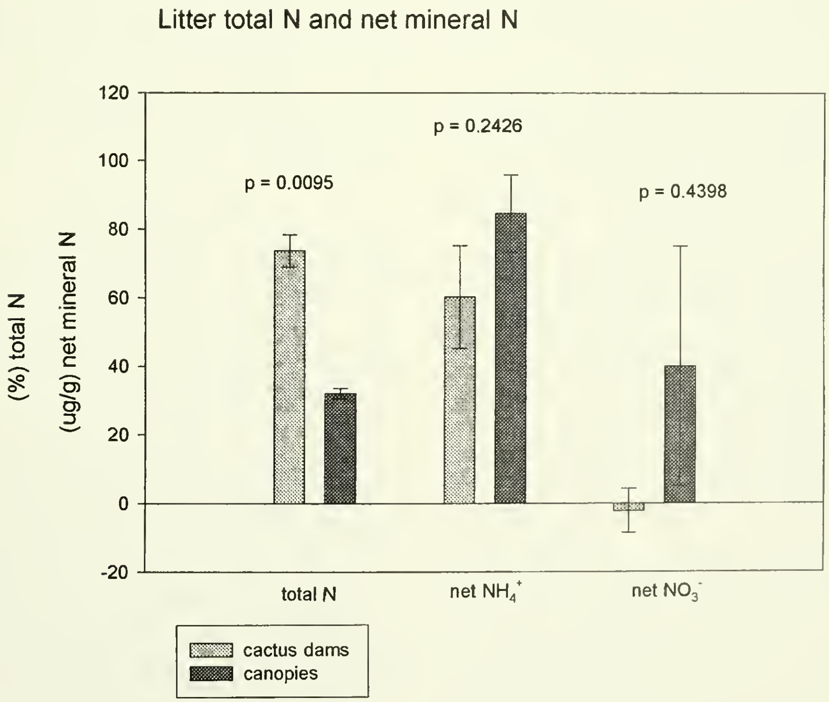

Fig. 5. Nitrogen in the litter accumulated above cactus dams compared with the litter layer beneath canopies (trees and shrubs combined).

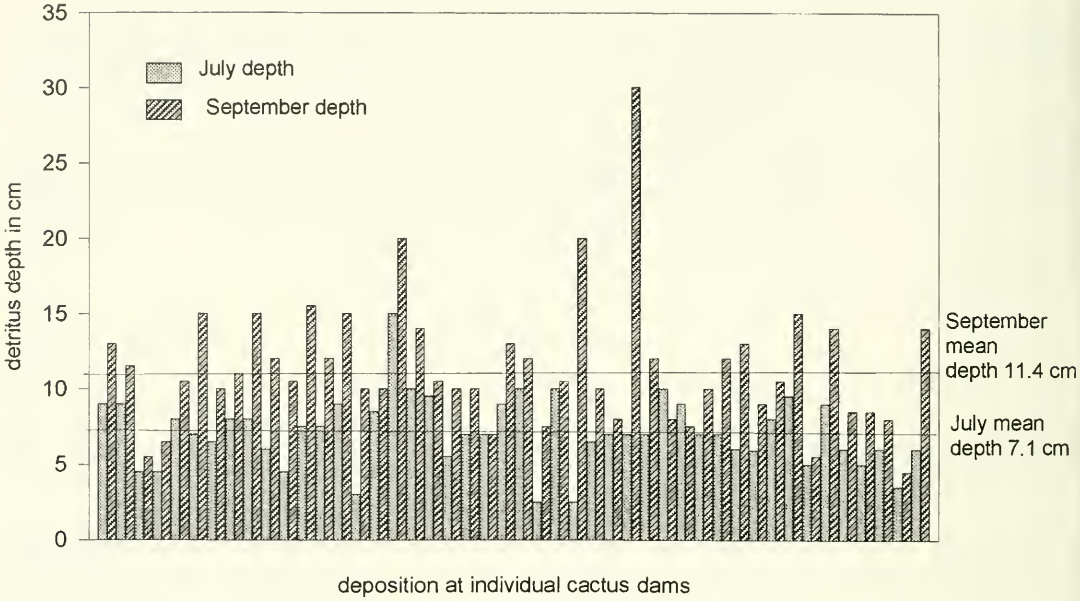

Fig. 6. Deposition at cactus dams during 1 season of summer thundershowers: depths of detritus accumulations at 46 cactus dams in July and in September.

1987, Nobel 1989). Increased productivity in desert prickly pear cacti is positively correlated with both number of new cladodes produced and cladode size (Nobel et al. 1987). We do not know if similar patterns occur in woodland species of prickly pear. Additionally, Nobel (1988) describes a tendency for "daughter" cladodes to replicate the orientation of "mother" cladodes and points out that if a particular direction of growth is favorable, it may be perpetuated. This happens because favorably oriented cladodes are expected to be more productive than other cladodes and produce more and larger similarly oriented cladodes. This may be occurring in dam-forming cacti, but it was not investigated in this study.

Cactus dams lower soil bulk density and enrich patches of woodland interspace with organic matter, total N, and net mineral N, suggesting that they may play roles in nutrient cycling and other ecosystem processes. Some possible functions of cactus dams are to (1) increase woodland detritus storage, (2) increase the rate of N turnover, (3) mitigate nutrient loss in interspace areas, (4) reduce soil erosion and dampen effects of disturbances, (5) provide seedbeds, and (6) provide habitat for other organisms.

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DISTRIBUTION AND ECOLOGICAL CHARACTERISTICS OF *LEWISIA LONGIPETALA* (PIPER) CLAY, A HIGH-ALTITUDE ENDEMIC PLANT

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ABSTRACT.—*Lewisia longipetala* (Piper) Clay is a high-altitude endemic found in the northern Sierra Nevada. The characteristics of 12 sites with *L. longipetala*, which represent all known populations, were studied to define habitat requirements of the species. Meso- and microscale characteristics of the habitat were examined, including characteristics of the associated plant community. Average plant size and plant density of *L. longipetala* were also determined for each population. Similar measurements were made on 6 populations of *Lewisia pygmaea* (A. Gray) Robinson, a more common *Lewisia*. Populations of *L. longipetala* that had larger plants and higher plant density were associated with gently sloped, north-facing sites that were near large, persistent snowbanks and had low vegetative cover. Plant species associated with populations of *L. longipetala* were similar among the 12 sites and were indicative of mesic, rocky alpine sites. These types of plant communities found near persistent snowbanks are often termed snow-bed vegetation. In contrast, *L. pygmaea* was found to be less site specific. *Lewisia pygmaea* was found adjacent to or interspersed with *L. longipetala* at 5 sites, but was found in areas associated with a higher percentage of herbaceous cover and a wider variety of species. This integration of ecological and community information for *L. longipetala* populations contributes to the interim management and long-term monitoring of this species by providing needed information concerning its habitat and environmental specificity.

Key words: Lewisia longipetala, Lewisia pygmaea, *site characteristics, snow-bed vegetation, alpine, endemic, plant size, plant density.*

The recent implementation of programs to preserve rare plant taxa indicates the elevated concern for effective and long-term stewardship of sensitive species (Sutter 1986). One of the initial steps toward the protection of rare plants is to document their occurrences (Utter and Hurst 1990). Mountain ranges are typically rich in endemics (Major 1989), and within the Sierra Nevada they comprise a high percentage of the flora (Stebbins and Major 1965). Factors that characterize the species' habitat are inferred from the species' geographic distribution and often suggest environmentally imposed limitations on the distribution of sensitive plant taxa (Baskin and Baskin 1988, Hutchings 1991, Nelson and Harper 1991). For example, some limitations that influence endemic plants within alpine environments are snowbank depth and duration (Komárková 1975, Webber et al. 1976) and levels of disturbance to root systems from needle ice (Fitzgerald et al. 1990). To help ensure the survival of rare plant species, habitat and biological information should be integrated with long-term monitoring programs (Sutter 1986, Baskin and Baskin 1988, Hutchings 1991).

Species within the genus *Lewisia* (Portulacaceae) are well known in horticulture (Elliot 1966, Mathew 1989). However, little information exists regarding these species in their native environments. Only 4 species within the genus *Lewisia* have relatively wide distributions: *Lewisia pygmaea* (A. Gray) Robinson, *L. nevadensis* (A. Gray) Robinson, *L. triphylla* (S. Watson) Robinson, and *L. rediviva* Pursh. The remaining 15 species have considerably smaller distributions, and 9 that occur in California are listed by the U.S. Fish and Wildlife Service as candidates for threatened or endangered status.

Lewisia longipetala (Piper) Clay is a federal candidate 2 species, which implies that data on identifiable threats are insufficient to support federal listing as threatened or endangered (Skinner and Pavlik 1994). *Lewisia longipetala* is an endemic species with limited distribution that the California Native Plant Society classifies as a category 1 B species, which is a category for rare, threatened, or endangered plants within California. *Lewisia longipetala* populations are fairly remote, and most exist in U.S. Forest Service wilderness areas. Although *L.*

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longipetala populations are not an immediate management concern, one population (Basin Peak) is on private land, and mining claims within close proximity of the site pose a potential threat. Furthermore, the potential also exists for activation of mining claims within wilderness areas as well as increased ski area development within the vicinity of the other *L. longipetala* populations.

The first specimen of *L. longipetala* was collected by J. G. Lemmon in 1875 in the mountains west of Truckee, California. In 1913, Piper described *L. longipetala* as *Oreobroma longipetalum*, an intermediate between *L. pygmaea* and *L. oppositifolia* (S. Watson) Robinson. Later descriptions (Munz 1959) placed *L. longipetala* as a subspecies of *L. pygmaea*. More recently, *L. longipetala* was again recognized as a distinct species (Dempster 1993), a distinction supported by morphological as well as chromosomal differences between *L. longipetala* and *L. pygmaea* (Stebbins 1968, Halford 1992).

Lewisia longipetala (Fig. 1) is an herbaceous perennial with a basal tuft of green, linear leaves. An individual plant produces numerous scapes, 30–60 mm long, each bearing 1–3 pale pink flowers with petals 11–20 mm long. The two sepals are distinctly fuchsia in color, 4–10

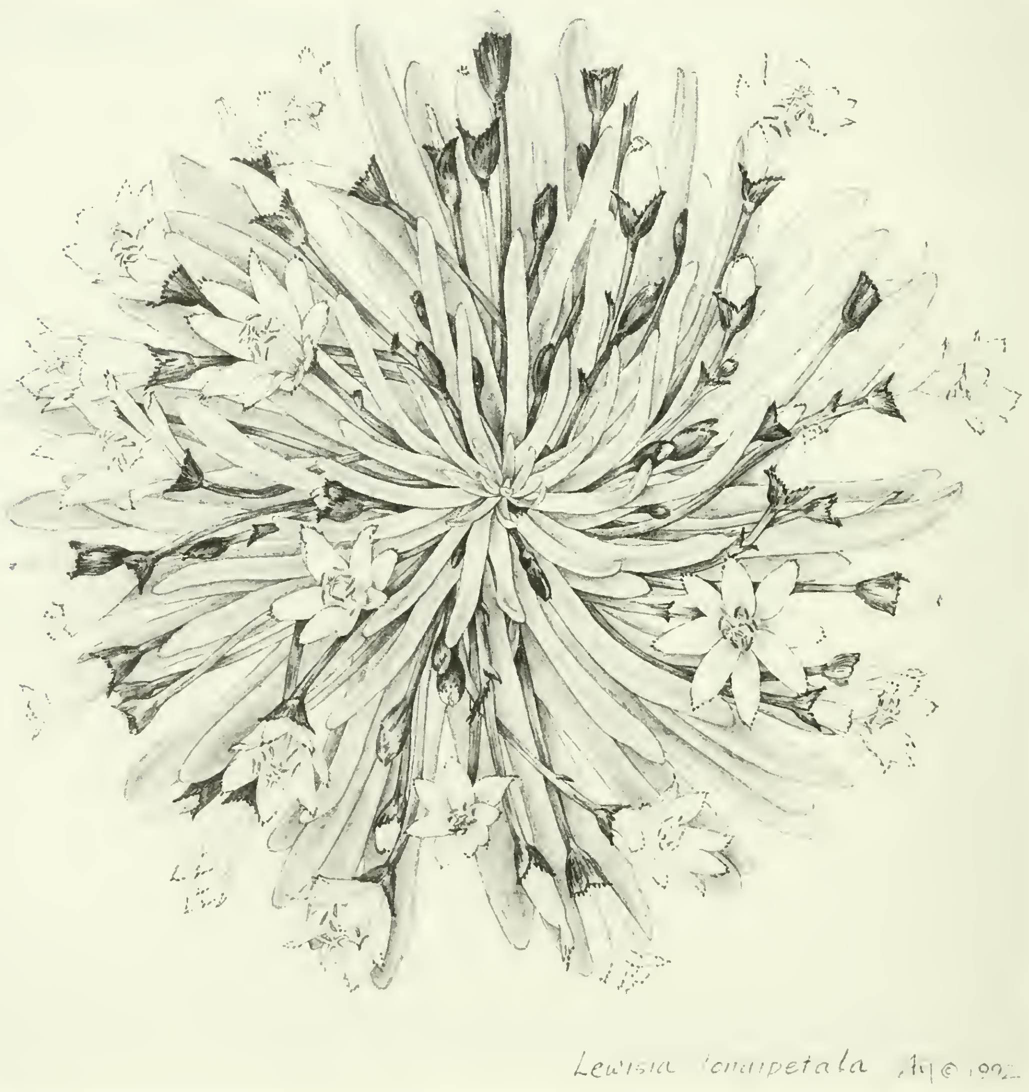

Fig. 1. Line drawing of *Lewisia longipetala* (Piper) Clay showing growth habit.

mm long, and conspicuously glandular-dentate (Elliot 1966, Mathew 1989). In contrast, inflorescences of *L. pygmaea* do not have pronounced scapes, and the flowers are smaller with petals 6–10 mm long. Flower color for *L. pygmaea* ranges from pink to white, and sepal color varies from green to fuchsia. For both species, seeds are similar in size (1.5 mm long), numerous (50–60) per capsule, and passively ejected as the capsule dehisces. However, *L. longipetala* seeds are black, whereas those of *L. pygmaea* are reddish brown.

The primary goal of this study was to integrate baseline ecological and community information for *Lewisia longipetala*. This information could then be used to (1) describe suitable habitat requirements, (2) provide necessary environmental criteria to search for additional populations of *L. longipetala*, and (3) establish guidelines for the interim management and long-term monitoring of this species. Potential factors that influence the size of individual plants and the occurrence and size of populations include environmental and community attributes such as elevation, slope, aspect, proximity to snowbanks, parent material, and percent cover of vegetation, surface rock, surface water, litter, and bare ground. To help delineate the habitat requirements of *L. longipetala*, 6 populations of *L. pygmaea*, which also occurs in alpine areas but is a more widespread *Lewisia*, were also studied. The 2 objectives of our study were (1) to determine environmental and community characteristics for *L. longipetala*, and (2) to determine correlations between the size of *L. longipetala* plants and site characteristics, such as elevation, slope, slope aspect, percent cover, and proximal location to snowbanks, as well as between plant density of *L. longipetala* populations and these site characteristics.

METHODS

A total of 12 *L. longipetala* populations (Fig. 2), which represent the total number of known populations of *L. longipetala*, were examined. Nine populations were determined from California Department of Fish and Game database maps; during this study 3 additional populations were located. Basin Peak populations 1 and 2 are the most northern populations, and the remaining 10 populations extend south through the Granite Chief and Desolation wilderness areas of the Sierra Nevada (Fig. 2). For more detailed measurements of *L. longipetala*, three 15 × 15-m plots were established at Basin Peak 1. In plot 1, plants of *L. pygmaea* were present but no plants of *L. longipetala* were present; plot 2 was adjacent to plot 1 and had plants of both *L. longipetala* and *L. pygmaea*; plot 3 was approximately 10 m north of plot 2 and also had both *Lewisia* species.

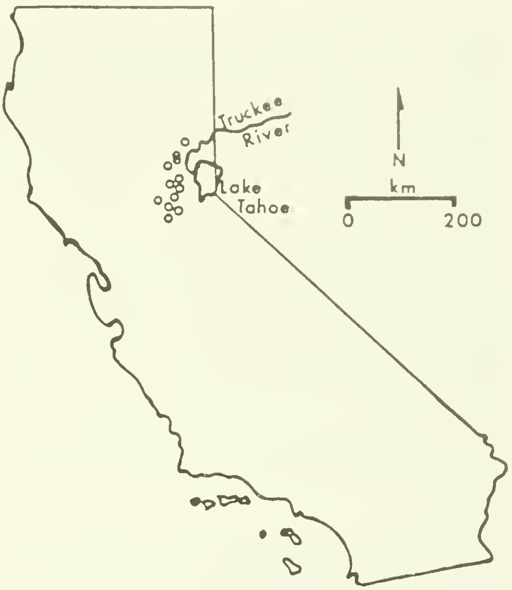

Fig. 2. Distribution of *Lewisia longipetala*: known populations of *L. longipetala* are indicated by open circles.

To help delineate the habitat requirements of *L. longipetala*, a total of 6 *L. pygmaea* populations were also sampled. Five of these populations (Basin Peak 1, Basin Peak 2, Granite Chief, Keith's Dome, and Dick's Lake) were selected because *L. pygmaea* plants were near or interspersed with *L. longipetala*. The 2 species were interspersed at Basin Peak 1 and Basin Peak 2, and measurements of *L. pygmaea* were made in areas that had predominantly *L. pygmaea*. At Granite Chief, Keith's Dome, and Dick's Lake, the distribution of the 2 species did not overlap; for these sites the population of *L. pygmaea* that was nearest the *L. longipetala* population was sampled. The 6th population of *L. pygmaea* was at Piute Pass, which is an area previously described as having *L. longipetala*, but where no *L. longipetala* plants were documented in this study.

For each population we collected a set of 9 site characteristics that included environmental characteristics (elevation, slope aspect, slope, and distance from nearest uphill snowbank) as well as more detailed community data (percent cover of rock, bare ground, litter, surface water, and vegetation by species). In addition, we also noted geologic parent material. To obtain the cover data, three 15-m transects were placed within each of the populations except Basin Peak 1. The starting point for all 3 transects was the geographic center of the population, and transects radiated out from this starting point along 3 randomly selected compass directions. At Basin Peak 1 the three 15-m transects were uniformly spaced along contours within each of the three 15 × 15-m plots. Cover values were obtained using a cover point projector (Model 2, ESCO and Associates, Inc., Boulder, CO).

Estimates of plant density were obtained by direct count of individuals within a 0.5-ha area until the number of individuals exceeded 500. The 0.5-ha area was orientated such that it encompassed the topographical extent of each population and was centered on the geographic center of the population. In addition, plant size was estimated from the clump diameter of an individual plant. Up to 20 *L. longipetala* individuals were selected for clump diameter measurements. If the population size was less than 20, all individuals were measured. If population size was greater than 20, then 20 individuals were chosen for measurement by randomly selecting 20 numbers between 0.0 and 15.0 (in 0.1 increments). These numbers represented sampling points along the transect tape: if 1 or more plants were within 1 m of the designated sampling point, then the plant nearest the designated sampling point was measured. If no plants were within 1 m of the sampling point, then additional sampling points were randomly selected for the 2nd and 3rd transects as necessary.

Regression analyses were used to determine correlations between plant density and the set of 9 site characteristics (elevation, slope, slope aspect, distance from nearest uphill snowbank, bare ground cover, litter cover, surface rock cover, surface water cover, and total vegetative cover) for *L. longipetala* as well as between clump diameter and the 9 site characteristics. The 1st regression analysis used multiple regressions to determine the 3 models that had the highest R^2 values for regressions with 1 site characteristic, the 3 models with the highest R^2 for regressions with 2 site characteristics, the 3 models with the highest R^2 with 3 site characteristics, and the 3 models with the highest R^2 with 4 site characteristics. Next, a series of forward stepwise regressions were performed that started with each of these 12 models. Finally, a backward stepwise regression was performed that started with all 9 site characteristics. Statistix Version 4.1 (Analytical Software, Tallahassee, FL) was used for all analyses. Results were considered significant if $P < 0.05$.

Vegetation Association Analyses

Floristic data were analyzed using multivariate methods that grouped populations based on the fidelity of species to a particular population or stand. Three different programs were used: (1) a 2-way indicator species analysis (TWINSPAN; Hill 1979a), (2) Detrended Correspondence Analysis (DCA; Hill 1979b), and (3) nonmetric multidimensional scaling program (NMDS). TWINSPAN and NMDS are classification programs that divide the plots into a series of groups based on percent similarity; NMDS differs from TWINSPAN in that NMDS recovers gradients of high beta diversity that may alter the ordering of samples (Minchen 1987). DCA is an ordination program that orders the plots along a series of axes such that the distance between plots in the multidimensional space is proportional to the differences between them. To graphically represent the results of the classification and ordination analyses, populations and species were plotted in the 2-dimensional space formed by DCA axes 1 and 2. Hierarchical classifications that were constructed from TWINSPAN eigen values were then used to draw the groupings of populations and species on the DCA plots; where NMDS groupings differed from TWINSPAN, NMDS grouping were also drawn.

To examine relationships between species composition and environmental site characteristics for these populations, we used a rotational correlation analysis to generate correlation coefficients between the DCA axis 1 scores and the site characteristic (Dargie 1984, Tueller et al. 1991). Correlation matrices were developed for the set of 9 site characteristics: elevation, slope, aspect, snowbank distance, total vegetative cover, surface rock cover, bare ground cover, surface water cover, and litter cover. For all correlation analyses, $P < 0.05$ was the level of significance used.

RESULTS

Lewisia longipetala

The majority of *L. longipetala* populations were in shallow, north-facing basins (Table 1). Fewer populations were on steep slopes or had a southern exposure. Most populations were between 2700 and 2900 m elevation, but *L. longipetala* populations were found up to 3200 m elevation. Populations were not restricted to only 1 rock type but were found on substrates derived from basaltic and granitic rocks. *Carex scopulorum* var. *bracteosa* and *Antennaria media* were the 2 species that co-occurred with most *L. longipetala* populations and had the highest mean cover (Table 2).

The largest populations of *L. longipetala* were on low-gradient, north- to northeast-facing sites (Table 1). Populations with lower densities were on steep slopes (>30%) with west-, southwest-, or southeast-facing slopes. Regression analyses between plant density and 9 site characteristics did not yield 1 "best" model but rather 2 models that had similar adjusted R^2 values (Table 3). For both models, slope was a significant dependent variable, and plant density was inversely correlated with slope (i.e., as slope increased, plant density decreased). Surface water and surface rock cover were significant dependent variables in 1 model, and plant density was positively correlated with both of these dependent variables. In the 2nd model, total vegetative cover was a significant dependent variable, and *L. longipetala* density was inversely correlated with vegetative cover.

Populations with the largest plants generally were also those with the highest plant density (Table 1). Regression analyses between clump diameter and 9 site characteristics yielded a single model that all forward and backward stepwise regressions converged upon (Table 3). Mean plant diameter from each population was inversely correlated with distance from the nearest uphill snowbank. The value of the regression coefficient for surface litter cover was significantly different from zero at the 6% probability level rather than the 5% level, and plant size was inversely correlated with the amount of surface litter cover.

Classification and ordination of the floristic data corroborated these results (Fig. 3). Four site characteristics were found to be significantly correlated with DCA axis 1 scores (Table 4), and these site characteristics are shown in Fig. 3A as vectors that indicate the directional increase of slope, surface rock cover, bare ground cover, and total vegetative cover. TWINSPAN classified the 12 populations into 3 groups (Fig. 3A), and the species groupings associated with the TWINSPAN population groupings are shown in Fig. 3B. The Basin Peak populations had higher vegetative cover, whereas the other populations had higher rock cover (Fig. 3A). These populations that are associated with increasing rock cover contain species such as *Antennaria media*, *Cassiope mertensiana*, and *Kalmia polifolia* var. *micropylla* that are indicative of such environments (Fig. 3B). *L. longipetala* populations at Granite Chief, Top Lake, Mt. Price 2, Mt. Price 3, and

TABLE 1. Descriptive site attributes for 12 *Lewisia longipetala* populations, ordered from north to south. Mean ± standard error of plant diameter from 20 randomly selected plants, as well as plant density, is given for each population.

Population	Parent material	Elevation (m)	Aspect	Slope (%)	Plant diameter (cm)	Plant density (# per 0.5 ha)
Basin Peak 1	Basalt	2800	NNE	2–8	9.7 ± 0.3	185
Basin Peak 2	Basalt	2840	NNE	2–8	3.9 ± 0.1	10
Pole Creek 1	Basalt	2733	NNE	2–6	13.0 ± 0.9	>500
Pole Creek 2	Basalt	2733	NNE	2–6	8.2 ± 0.4	>500
Granite Chief	Granite	2800	N	>30	6.5 ± 0.1	135
Dick's Lake	Granite	3033	NNE	2–10	8.6 ± 0.4	>500
Top Lake	Granite	2866	W	>30	4.2 ± 0.2	12
Mt. Price 3	Granite	3133	WSW	>30	6.3 ± 0.4	35
Mt. Price 1	Granite	3200	SSE	2–8	3.4 ± 0.2	40
Keith's Dome	Granite	2800	NNE	2–8	10.8 ± 0.4	>500
Mt. Price 2	Granite	2966	SSW	>30	8.3 ± 0.3	30
Pyramid Peak	Granite	2787	WNW	>30	4.1 ± 0.2	25

TABLE 2. Mean percent cover for species found within *Lewisia longipetala* populations and the number of *L. longipetala* populations that contained that species. Species are listed from highest to lowest cover. Hickman (1993) was used as the authority for all species. Letter codes used in Figures 3 and 4 are given in brackets for each species.

Species	Species code	Mean cover	# of pop.
Carex scopulorum Holm. var. *bracteosa* (L. Bailey) F. Herm.	[Casch]	6.2	9
Antennaria media E. Greene	[Anme]	5.1	9
Juncus mertensianus Bong.	[Jume]	4.2	4
Erigeron peregrinus (Pursh) E. Greene	[Erpe]	2.9	2
Lupinus breweri A. Gray	[Lubr]	2.6	1
Lewisia pygmaea (A. Gray) Robinson	[Lepy]	1.9	5
Lewisia longipetala (Piper) Clay	[Lelo]	1.7	12
Arnica mollis Hook.	[Armo]	1.4	1
Mimulus guttatus DC.	[Migu]	1.2	3
Salix artica Pallus	[Saar]	1.2	3
Aster alpigenus (Torrey & A. Gray) A. Gray ssp. *andersonii* (A. Gray) M. Peck	[Asala]	1.0	5
Calyptridium umbellatum (Torrey) E. Greene	[Caum]	0.9	4
Phleum alpinum L.	[Phal]	0.9	2
Juncus drummondii E. Meyer	[Judr]	0.8	3
Sibbaldia procumbens L.	[Sipr]	0.8	4
Dodecatheon alpinum (A. Gray) E. Greene	[Doal]	0.7	2
Cassiope mertensiana (Bong.) Don	[Came]	0.7	2
Kalmia polifolia Wangenh. ssp. *microphylla* (Hook.) Calder & Roy Taylor	[Kapom]	0.5	2
Lycopodium sp.	[Lycsp]	0.5	5
Mimulus primuloides Benth.	[Mipr]	0.5	3
Poa wheeleri Vasey	[Powh]	0.3	1
Polygonum bistortoides Pursh	[Pobi]	0.3	2
Eriogonum incanum (Torrey & A. Gray)	[Erin]	0.2	1
Penstemon rydbergii Nelson ssp. *oreocharis* (E. Greene) N. Holmgren	[Peryo]	0.2	1
Phyllodoce breweri (A. Gray) Maxim.	[Phbr]	0.2	2
Anemone drummondii S. Watson	[Andr]	0.1	1
Poa secunda J.S. Presl ssp. *secunda*	[Poses]	0.1	1
Sedum roseum (L.) Scop. ssp. *integrifolium* (Raf.) Hulten	[Seroi]	0.1	1

Pyramid Peak were situated in cracks on steep granitic slabs, and one of the most common species found associated with these sites was rock sedum (*Sedum roseum* ssp. *integrifolium*). NMDS results differed slightly from the TWINSPAN classification by the separation of the Top Lake population from all other populations and by a change in association of the Basin Peak 2 population from the group of 3 Basin Peak 1 plots to the group of 7 plots to the right of Basin Peak 2. In the 2-dimensional space defined by DCA axes 1 and 2, Basin Peak 2 appears to be transitional in its floristic composition between the Basin Peak 1 plots and this group of 7 populations. Species that contributed to these different classifications of the Basin Peak populations were *Phleum alpinum* and *Lupinus breweri*: *P. alpinum* was within

TABLE 3. Multiple regression results between each of 2 dependent variables (plant density and plant diameter) and the set of 9 site characteristics for 12 *Lewisia longipetala* populations.

	Regression statistics				Variable statistics	
Dependent variable	*N*	adj. R^2	*P*	Model variables	Coefficient	*P*
Plant density	12	0.81	<0.01	Slope	–18.5	<0.01
				Surface water cover	11.2	<0.01
				Surface rock cover	6.9	0.01
	12	0.81	<0.01	Slope	–16.6	<0.01
				Total vegetative cover	–6.5	<0.01
Plant diameter	12	0.53	0.01	Snowbank distance	–0.07	<0.01
				Surface litter cover	–0.24	0.06

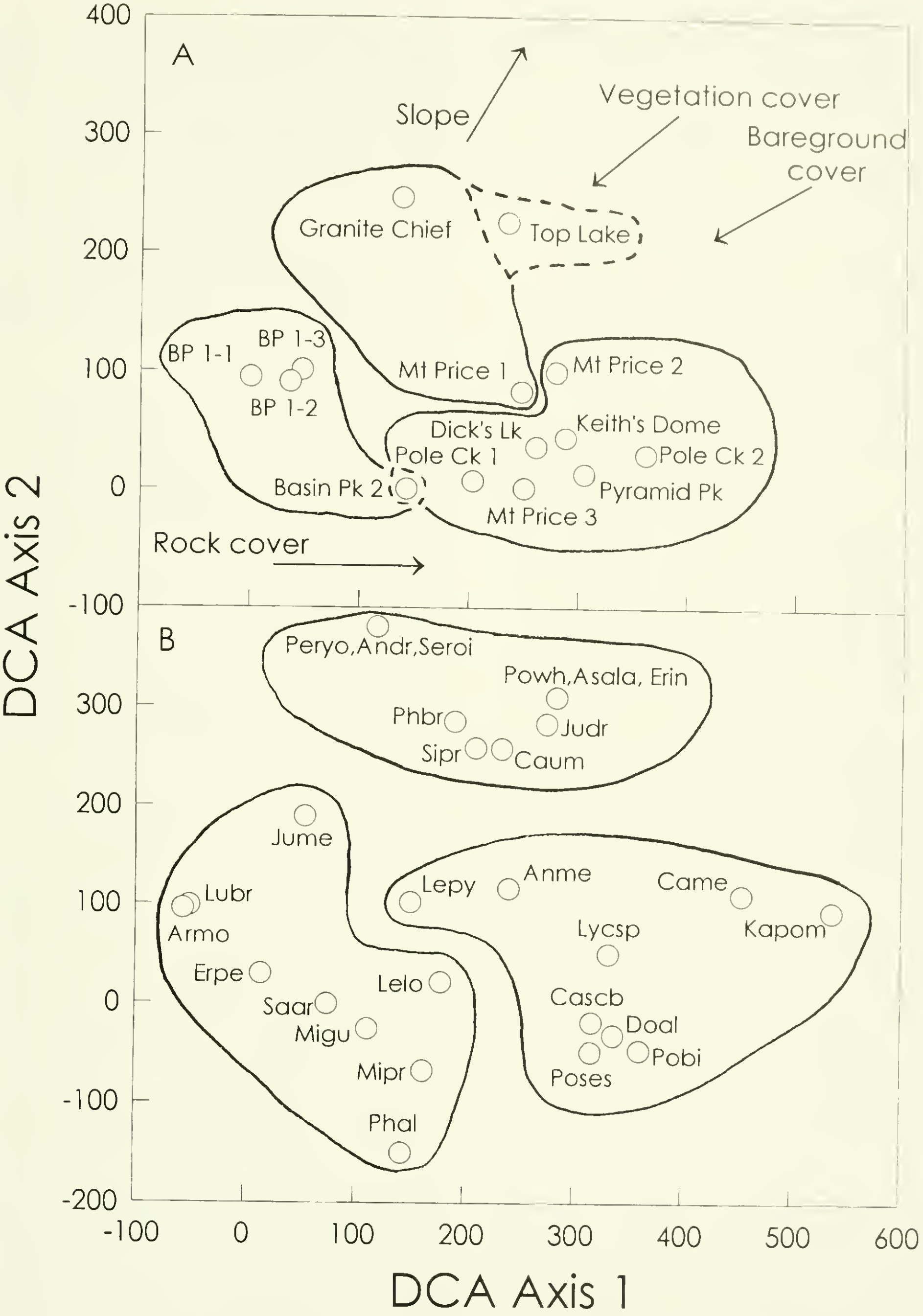

Fig. 3. A, Population ordinations generated by DCA for *L. longipetala;* B, species groupings associated with the populations. For both graphs, circled groups were determined from TWINSPAN dendrograms; broken lines indicate NMDS groupings. Letter codes for each species are given in Table 2.

TABLE 4. Correlation coefficients generated from a rotational correlation program for all *Lewisia longipetala* and *Lewisia pygmaea* DCA axis 1 scores. Variables with an * are significant at the 0.05 level.

Species Variables	Correlation coefficients
Lewisia longipetala	
Elevation	0.24
*Slope	–0.58
Aspect	–0.49
Snowbank distance	0.41
*Bare ground cover	0.66
Litter cover	0.36
*Surface rock cover	0.71
Surface water cover	0.11
*Total vegetative cover	0.67
Lewisia pygmaea	
Elevation	–0.53
Slope	0.17
Aspect	–0.14
Snowbank distance	0.38
*Bare ground cover	0.92
*Litter cover	0.92
Surface rock cover	0.34
Surface water cover	0.26
*Total vegetative cover	0.78

the sampled transects of both Basin Peak 1 and 2 populations but not within any of the other populations; on the other hand, *L. breweri* was only within the Basin Peak 1 populations. In general, it should be noted that classification inferences based solely on location within the 2-dimensional space defined by any 2 DCA axes can be misleading: for example, Mt. Price 1 and Mt. Price 2 are close together in the 2-dimensional space defined by DCA axes 1 and 2, but they do not classify into the same group in either TWINSPAN or NMDS because they are on different planes in the 3-dimensional space defined by the addition of a 3rd axis.

Lewisia pygmaea

Lewisia pygmaea grew in areas where total vegetative cover was greater than that where *L. longipetala* was found. The strongest evidence for this difference in site characteristics was from the 5 sites where *L. longipetala* and *L. pygmaea* coexisted in proximity to each other: Basin Peak 1, Basin Peak 2, Granite Chief, Dick's Lake, and Keith's Dome. Total vegetative cover for areas with *L. pygmaea* averaged 60.4 ($s_{\bar{x}}$: 5.9), which was 55% greater than the mean cover of 39.0 ($s_{\bar{x}}$: 12.3) for areas with *L. longipetala*; this difference was significant at $P < 0.10$ (paired *t* test, 4 d.f., $P = 0.067$). This large difference in vegetative cover persisted even when all populations were considered: for all the known *L. longipetala* populations, mean vegetative cover was 31.8 ($s_{\bar{x}}$: 5.8); for the 6 *L. pygmaea* populations used in this study, mean vegetative cover was 53.7 ($s_{\bar{x}}$: 8.3). Although this difference was significant (2-sample *t* test, 16 d.f., $P = 0.046$), note that our original selection of *L. pygmaea* populations was not designed to be a random sample of all *L. pygmaea* populations and thus extrapolation to all *L. pygmaea* populations is not statistically justified.

TWINSPAN results for *L. pygmaea* populations grouped the Basin Peak populations separately from other populations (Fig. 4A), but the environmental site attributes that were significantly correlated with DCA axis 1 scores differed between *L. pygmaea* and *L. longipetala* (Table 4). Litter cover was a significant site attribute for *L. pygmaea*, but slope and surface rock cover were not. The vegetative cover vector increased toward the Basin Peak population, which suggested that these populations contained a greater herbaceous component. The species indicative of such areas include *Erigeron peregrinus*, *Salix artica*, and *Arnica mollis* (Fig. 4B). The bare ground vector also increased toward the Basin Peak stands. Although the concomitant increases in bare ground and vegetative cover may seem contradictory, surface rock cover tended to decrease toward Basin Peak. Thus, surface rock was replaced by vegetation and bare ground (i.e., inorganic soil) along these vectors. High litter cover was commonly associated with the Granite Chief and Keith's Dome populations.

Piute Pass is an area historically thought to contain *L. longipetala*. However, only *L. pygmaea* individuals were verified at this site. The area is south of Yosemite National Park, California, which makes it the southernmost site surveyed for *L. longipetala*. Environmental attributes of Piute Pass are similar to those of other *L. longipetala* and *L. pygmaea* populations, except for some differences in species composition, namely the relative preponderance of *Dodecatheon jeffreyi*.

DISCUSSION

Site characteristics that were most highly associated with the occurrence of *L. longipetala* and also correlated with plant size and

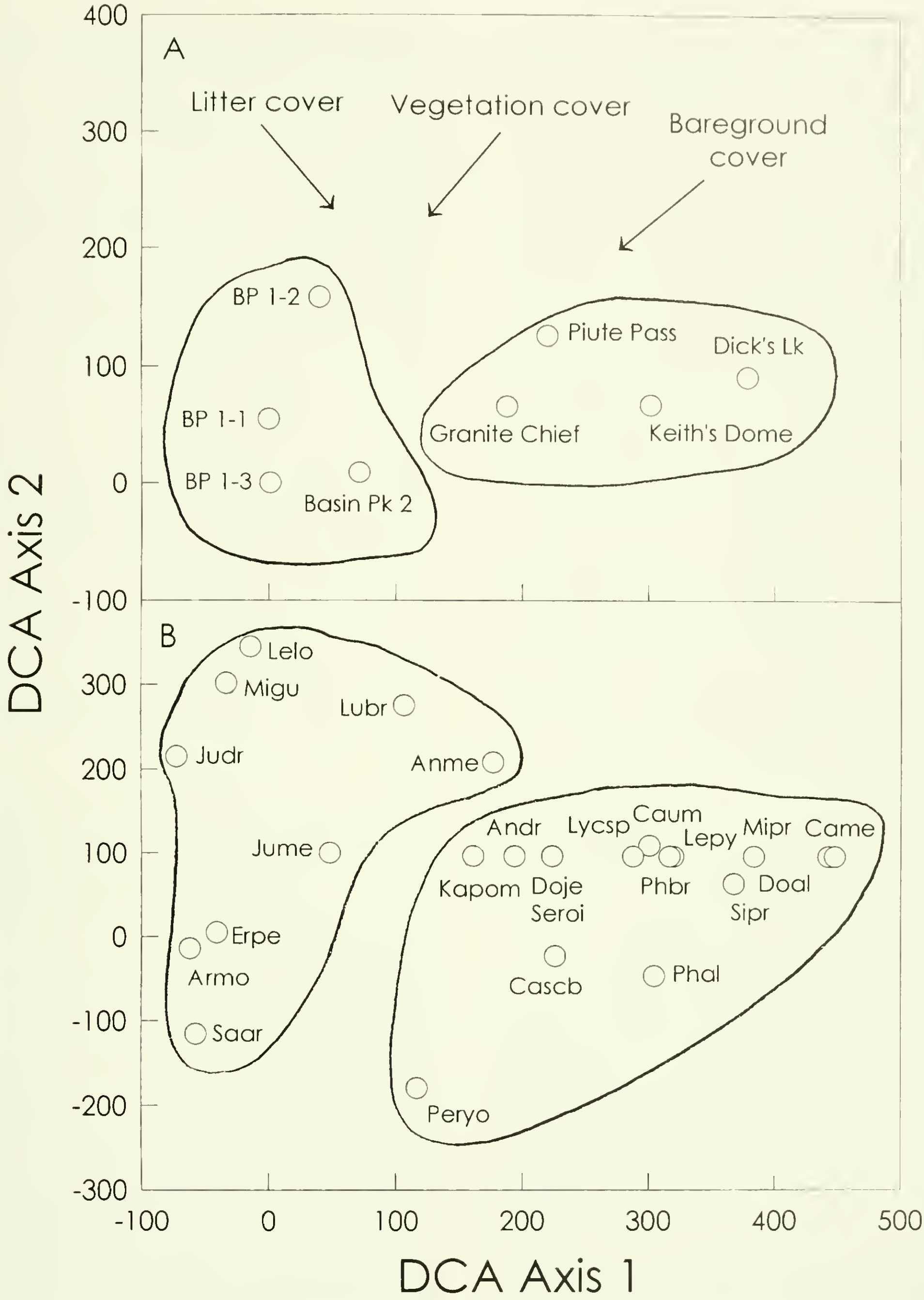

FIG. 4. A, Population ordinations generated by DCA for *L. pygmaea*; B, species groupings associated with the populations. For both graphs, circled groups were determined from TWINSPAN dendrograms. Letter codes for each species are given in Table 2, except Doje = *Dodecatheon jeffreyi*.

density were proximity of snowbanks, steepness of slope, slope aspect, and cover of vegetation, surface rock, and surface water. These inferences are supported by inspections of the site characteristics and by statistical analyses. The *L. longipetala* populations with higher density were found on gently sloping sites with a northern exposure that were close to snowbanks and had low vegetative cover of all species. For example, Pole Creek 1 and 2, Keith's Dome, and Dick's Lake have populations that exceeded 500 individuals, whereas Basin Peak, which overall had the most herbaceous cover of any of the other populations, had much lower plant density. Plant density of *L. longipetala* populations increased with increased cover of surface water and rock, but decreased with total vegetative cover and slope steepness. Plant size, as measured by clump diameter, increased with decreased distance from snowbanks and decreased litter cover. Furthermore, at Basin Peak 1 as well as other sites of *L. longipetala* populations, plants that were more distant from snowbanks or that were on south-facing slopes were more water stressed (Halford 1992).

Site characteristics that are associated with more vigorous *L. longipetala* populations are indicative of areas that receive high snowpack accumulations. In alpine environments plant communities whose occurrences are influenced by geomorphological characteristics that favor high snowpack accumulations are often termed snow-bed vegetation (Billings and Bliss 1959, Kuramoto and Bliss 1970, Canaday and Fonda 1974, Tomaselli 1991). Some species in the Sierra Nevada that Major and Taylor (1977) commonly found associated with areas of high snowpack accumulations and that often occur in mesic depressions with low vegetative cover are *Phyllodoce breweri*, *Cassiope mertensiana*, *Kalmia polifolia* var. *microphylla*, *Phleum alpinum*, *Mimulus primuloides*, and *M. guttatus*. Additional species that occur in mesic to even hydric habitats include *Antennaria media*, *Sibbaldia procumbens*, *Dodecatheon alpinum*, and *Sedum roseum* (Major and Taylor 1977). These species were also associated with *L. longipetala* populations. Conversely, species that are more frequently associated with xeric sites, such as *Lupinus breweri* and *Juncus drummondii* (Chabot and Billings 1971, Nachlinger 1985), were less frequently associated with *L. longipetala* populations.

The restriction of some species to sites with low vegetative cover may be related to reduced interspecific competition (Ostler et al. 1982). For example, competition partially accounts for the reduced growth of *Talinum calcaricum*, a highly restricted rock outcrop species of the Portulacaceae family, in herbaceous sites dominated by *Poa pratensis* (Ware 1991). Viable populations of the endangered Furbish's lousewort (*Pedicularis furbishiae*) occur on mesic, rocky sites that experience intermediate disturbances from hydrological processes, which remove potential competitors (Menges 1990). *Potentilla robbinsiana*, an endemic from New Hampshire's White Mountains, also requires rocky mesic sites that are moderately disturbed, in this case by frost heaving that limits other species (Fitzgerald et al. 1990). The lower densities and smaller *L. longipetala* plants in areas with high vegetative cover and high soil organic matter (Halford 1992) suggest that interspecific competition may also restrict this species, but specific studies need to be conducted to explicitly test this mechanism.

The environmental site characteristics of *L. pygmaea* are broader than those of *L. longipetala*. Populations of *L. pygmaea* have been documented in dense herbaceous meadows, cracks in steep rocks, and open gravely depressions (Elliot 1966, Major and Taylor 1977). In our study, plants of *L. pygmaea* were found adjacent to 3 and interspersed with 2 of the 12 *L. longipetala* populations, which suggests that *L. pygmaea* and *L. longipetala* can grow in similar environments. However, an important difference between the 2 species is that *L. pygmaea* was found in areas with more herbaceous cover. The less pronounced site specificity exhibited by *L. pygmaea* parallels other widely distributed, mesic alpine species, whereas the relative restriction of *L. longipetala* to more open sites is similar to other restricted plant taxa (Fitzgerald et al. 1990, Menges 1990).

The potential threats to *L. longipetala* are not imminent at this time but include both stochastic and anthropogenic processes. Climatic events such as periodic droughts that reduce snowpack accumulations as well as potential increases in interspecific competition may significantly reduce the viability of *L. longipetala* populations, especially those that already have low densities of individuals. Human activities may also have significant impacts. For example, if slopes above populations are altered by mining activity or ski area development, the displacement of substrate could alter the topography and hence hydrology of the site through changes in snow accumulation and melt water runoff. To enhance the long-term viability of this endemic species, primary management goals should include (1) monitoring of *L. longipetala* populations to gauge how changes in site hydrology may influence fluctuations in plant density and (2) acquisition by land conservation groups of sites that may be impacted due to mining or ski area development.

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LARGER ECTOPARASITES OF THE IDAHO GROUND SQUIRREL (*SPERMOPHILUS BRUNNEUS*)

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ABSTRACT.—We sampled both subspecies of the Idaho ground squirrel (*Spermophilus brunneus*) to document the larger ectoparasites of this rare endemic. *S. b. brunneus* was host (+ = new host record, * = new Idaho record) to 4 flea species (*Neopsylla inopina*+, *Oropsylla idahoensis*+, *O. tuberculata*, and *Thrassis pandorae*+), 1 tick (*Ixodes sculptus*+), and an eyeworm (Nematoda: *Rhabditis orbitalis**+, also 1st records from Sciuridae); *S. b. endemicus* was host to a louse species (*Neohaematopinus laeviusculus*+), 5 flea taxa (*Rhadinopsylla* sp.+, *O. t. tuberculata*, *Thrassis f. francisi*+, *T. f. barnesi*+, and *T. f. rockwoodi*), and a mite (*Androlaelaps fahrenholzi*+). *Spermophilus brunneus* had fewer known ectoparasite species than other congeners. Although all of their parasites had many other hosts, *S. b. endemicus* and *S. b. brunneus* shared only a single parasite species in common, whereas all but one of their ectoparasites also occurred on the closely related Townsend's ground squirrel (S. *townsendii*). The proportion of parasitized individuals and the parasite loads per individual were significantly lower in *S. b. brunneus*, which lives in small, isolated populations, than in *S. b. endemicus*, which has larger, less fragmented populations, suggesting a relationship between host population structure, parasite loads, and parasite species diversity. All but one of the flea species have been linked to plague transmission.

Key words: ground squirrels, ectoparasites, Spermophilus brunneus, *Idaho.*

The Idaho ground squirrel (*Spermophilus brunneus*) is one of the rarest and, until recently, least known North American mammals (Sherman 1989, Yensen 1991, Yensen and Sherman in press). This endemic species inhabits a 125 × 90-km area in west central Idaho, but it actually occupies only a small fraction of this limited range (Yensen 1991). Despite the species' restricted geographic distribution, there are 2 allopatric subspecies that are morphologically and genetically differentiated and possibly have reached species-level separation (Yensen 1991, Gill and Yensen 1992, Gavin et al. submitted).

Spermophilus b. brunneus occurs in montane meadows surrounded by coniferous forests at elevations of 1035 to 1550 m in Adams and Valley counties (Yensen 1991). As of 1995, only 18 of the 28 known populations remained, and only one of these contained >100 animals. The majority of the sites were within an area of 22 × 9 km and totaled <300 ha of occupied habitat (T. A. Gavin, P. W. Sherman, and E. Yensen unpublished data).

Fire supression began in the area about 100 yr ago. Subsequent succession and expansion of forests has filled in many of the natural meadows in the range of *S. b. brunneus* (Truksa and Yensen 1990), eliminating habitat. The remaining populations are presently isolated from each other by the encroachment of conifers into meadows and by competition with Columbian ground squirrels (Yensen and Sherman in press). Today, there is apparently little or no gene flow among populations. Allozyme analyses of 55 protein loci in 12 populations (Gavin et al. submitted) indicated that the proportion of polymorphic loci was 11.5%–19.2% and heterozygosity values were 0.041–0.080. F_{st} was 0.317, implying that there is genetic differentiation among populations despite their geographic proximity and the apparent recency of their separation. In 1993 the total number of individual *S. b. brunneus* was 1000–1200, but the number fell to 600–800 in 1994 and 1995 (T. A. Gavin, P. W. Sherman, E. Yensen personal observation).

Spermophilus b. endemicus occurs in rolling foothills at elevations of 670 to 975 m in Gem, Payette, and Washington counties (Yensen 1991). It is patchily distributed throughout its range of 75 × 30 km. Although censuses of *S. b. endemicus* populations have not been made, its total population is apparently much larger than that of *S. b. brunneus*. The area occupied, estimates of population densities, and the amount of remaining habitat are more than 2 orders of magnitude greater than for *S. b. brunneus* (E. Yensen personal observation).

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Parasites of *S. brunneus* have not been previously surveyed. The only prior records (Baird and Saunders 1992) were 2 flea species, *Oropsylla t. tuberculata* and *Thrassis francisi rockwoodi*, collected from specimens now referred to *S. b. endemicus* (Yensen 1991).

We were interested in how ectoparasite diversity and density are affected by reduction in size and isolation of host populations. According to epidemiological models (Anderson and May 1979, May and Anderson 1979), the number of contacts between hosts and infective stages of parasites determines the rate at which adult parasites are acquired. Mean parasite load should equal growth rate of the population divided by mortality from the disease. Thus, as population growth slows, parasite load per individual should drop. At very low host population densities, there may be too few contacts even to maintain ectoparasite populations. Thus, we predicted that *S. b. brunneus* should have fewer ectoparasite species and fewer ectoparasites per individual than congeneric, more widely distributed western ground squirrels (*Spermophilus* spp.). We also predicted that due to its fragmented population structure and smaller population sizes, *S. b. brunneus* should have fewer ectoparasite species than *S. b. endemicus*.

Because of questions about the taxonomic similarity of *S. b. brunneus* and *S. b. endemicus*, we also wished to learn if they had similar ectoparasites, and how similar their ectoparasites were to those of other western ground squirrels. Further, because of the limited geographic range and low number of small populations, both subspecies of *S. brunneus* would be vulnerable to extirpation by an epizootic such as plague. Thus, it was important to learn if their ectoparasites were species involved in plague transmission.

METHODS

From 1980 to 1990, specimens of *S. brunneus* were collected for a taxonomic study (Yensen 1991). To minimize negative impacts on small populations, a mean of 0.5 individuals/site/yr of *S. brunneus* was collected. Squirrels were killed by shooting or by live-trapping and injecting nembutol into the heart. Immediately postmortem, squirrels were placed individually in plastic bags; fleas, ticks, lice, and larger mites were collected with forceps or a camel's hair brush moistened with 70% ethanol as they left the host. Squirrels were not examined under a dissecting microscope, so smaller mites were not collected; eyes were not examined for eyeworms.

From 1987 to 1994, *S. b. brunneus* were live-trapped for demographic and behavioral studies (Sherman 1989, and ongoing). They were hand-held and parasites were picked off with forceps; because the animals were not anesthetized, all of the smaller and some of the larger ectoparasites may not have been seen. Eyes were checked for eyeworms by pulling back the upper lid; specimens were removed from the cornea of the eye with a cotton swab moistened with sterile water. All parasites were placed in 70% ethanol. In addition, 21 *S. b. endemicus* were live-trapped at Sand Hollow, Payette County, Idaho, in 1994 and examined for eyeworms.

Collected specimens of *S. brunneus* were prepared as standard museum study skins and skulls and deposited in the Albertson College Museum of Natural History (ACMNH), Caldwell, Idaho, and the National Museum of Natural History (USNM); they are identified below by museum number. Specimens of ectoparasites were sent to appropriate specialists for identification and deposited in the entomological collections at the University of Idaho, Moscow, and ACMNH. Differences in parasite loads between individuals and subspecies were analyzed with hand-calculated Mann-Whitney *U*-tests and chi-square tests, as appropriate.

RESULTS

We examined 29 freshly collected individuals of *S. b. brunneus* and 53 of *S. b. endemicus* for ectoparasites. These represent 43% of the 192 museum specimens of this species known to us (Yensen 1991, plus 4 additional specimens). Additionally, we opportunistically collected ectoparasitic arthropods from 12 live-trapped individuals of *S. b. brunneus* and eyeworms from another 36; we examined 21 *S. b. endemicus* for eyeworms.

We collected 6 ectoparasite species from *Spermophilus b. brunneus*: 4 fleas, 1 tick, and 1 nematode (Table 1). We collected 7 taxa of ectoparasites from *S. b. endemicus*: 5 fleas, 1 louse, and 1 mite.

TABLE 1. Parasites of *S. brunneus* that also occur on some other species of western ground squirrels (subgenus *Spermophilus*). Symbols: * = known primary host(s); + = records, possibly accidental on host; – = no records in references below[a].

	Host									
	This study		Literature records[b]							
Parasite	Sbb	Sbe	Sto	Scc	Sbl	Sar	Sel[c]	Sri	Swa	Spy
LICE										
Neohaematopinus laeviusculus	–	+	+	+	–	+	+	+	–	+
FLEAS										
Neopsylla inopina	+	–	+	+	+	+	+	+	–	–
Oropsylla idahoensis	+	–	+	*	*	*	*	+	–	*
O. t. tuberculata	+	+	+	+	+	+	–	+	+	–
Rhadinopsylla s. sectilis	–	?	+	–	–	–	–	–	+	–
Thrassis f. barnesi	–	+	+	–	–	+	+	–	–	–
T. f. francisi	–	+	*	–	+	+	–	–	–	–
T. f. rockwoodi	–	+	+	–	*	–	+	–	–	–
T. p. pandorae	+	–	+	+	*	*	*	+	+	–
TICKS										
Ixodes sculptus	+	–	+	+	+	+	+	+	–	–
MITES										
Androlaelaps fahrenholzi	–	+	+	+	–	+	+	+	–	+
NEMATODA										
Rhabditis orbitalis	+	–	–	–	–	–	–	–	–	–

[a] From records in Hubbard (1947), Burgess (1955), Stark (1970), Hilton and Mahrt (1971), Whitaker and Wilson (1974), Holekamp (1983), Lewis et al. (1988), Baird and Saunders (1992), Baird (unpublished), and this study.

[b] Host acronyms: Sbb = *Spermophilus b. brunneus*, Sbe = *S. b. endemicus*, Sto = *S. "townsendii"* (sensu latu), Scc = *S. columbianus*, Sbl = *S. beldingi*, Sar = *S. armatus*, Sel = *S. elegans*, Sri = *S. richardsonii*, Swa = *S. washingtoni*, Spy = *S. parryii*.

[c] Confused in the literature with *S. richardsonii*. The records here are those that unambiguously refer to this species, and the total for *S. richardsonii* may include a few parasites of this species.

The proportion of parasitized individuals in the 2 subspecies was strikingly different. We found ectoparasites on 37 of 53 (70%) *S. b. endemicus* but on only 8 of 29 (28%) *S. b. brunneus* collected ($\chi^2 = 13.4$, d.f. = 1, $P < 0.001$).

Parasitized individuals of *S. b. brunneus* had 1–3 species of ectoparasites each ($\bar{X} = 1.75$, $n = 8$), and parasitized individuals of *S. b. endemicus* had 1–4 species of ectoparasites ($\bar{X} = 1.59$, $n = 37$). This difference was not significant ($U_s = 154$, $P > 0.5$). However, there was a significant difference between subspecies in the parasite load of parasitized individuals. Fleas were the only common group of ectoparasites of both ground squirrel taxa. There were 4.1 fleas per parasitized individual in *S. b. brunneus* and 7.8 in *S. b. endemicus* ($U_s = 95.5$, $P < 0.05$).

ANNOTATED LIST OF ECTOPARASITES

In the ectoparasite species accounts below, letters and numbers in brackets refer to the number of male and female fleas, e.g., [1 m, 2 f], or to conversions of original collecting data to latitude, longitude, and metric units.

Anopleura: Haematopinidae

Neohaematopinus laeviusculus (Grube)

We found this louse on *S. b. endemicus* in the following locations: 11 mi [18 km] N Emmett, Gem Co., T8N, R2W, Sec. 13 [44°02′N, 116°31′W, 830 m elev.], 21 February 1982 (ACMNH 222), 28 February 1982 (ACMNH 226, 227, 236, 237, 238); 0.1 mi E Payette Co. line, 12.6 mi [20 km] N Emmett, Gem Co., T8N, R2W, Sec. 12 [44°03′N, 116°32′W, 810 m elev.], 28 February 1982 (ACMNH 224); Weiser Cove, Washington Co. [44°13′N, 116°44′W, 715 m elev.], 7 March 1982 (ACMNH 228, 229, 230); lower Mann Creek, 2.5 mi [4 km] N jct. Weiser River Road, Washington Co. [44°16′N, 116°51′W, 720 m elev.], 14 March 1982 (ACMNH 231, 240, 242, 243, 244).

This louse occurs from Eurasia east to Alaska and the Northwest Territories, and south through western United States to Mexico; it is apparently a species complex (K. C. Emerson personal communication). Lice of this complex have been collected from many ground squirrels (Eurasian *Spermophilus major, S. citellus, S. pygmaeus, S. undulatus,* and North American

S. beecheyi, S. armatus, S. beldingi, S. columbianus, S. parryii, S. townsendii, S. washingtoni, and *Ammospermophilus leucurus*), as well as marmots (*Marmota flaviventris*), chipmunks (*Tamias minimus*), pocket mice (*Perognathus parvus*), and deer mice (*Peromyscus maniculatus*; Rayburn et al. 1975, Shaw and Hood 1975, records from National Museum of Natural History). Although *N. laevinsculus* is the most common louse species taken from ground squirrels in Idaho (C. R. Baird personal communication, K. C. Emerson personal communication), *S. b. endemicus* is a new host record.

Siphonaptera: Hystrichopsyllidae

Neopsylla inopina Rothschild

We collected 8 individuals of this flea from *S. b. brunneus* in the following locations: Lick Creek, Adams Co., T19N, R3W, Sec. 14 [44°59′N, 116°40′W, 1290 m elev.], 17 April 1983 (ACMNH 305 [1 m, 2 f], ACMNH 306 [1 f]); 1 mi [1.6 km] NE Bear Guard Station, Adams Co. [45°05′N, 116°37′W, 1480 m], 2 June 1988 (ACMNH 518 [1 f]); and Price Valley [45°01′N, 116°26°W, 1270 m elev.], 3 June 1981 (ACMNH 209 [1 m, 1 f], ACMNH 210 [1 f]).

This flea occurs from British Columbia south to Oregon and Nevada and east to Saskatchewan, North Dakota, and Utah (Lewis et al. 1988). It has been collected from other western ground squirrels of subgenus *Spermophilus* (Table 1) and from badger (*Taxidea taxus*) dens (Lewis et al. 1988, Baird and Saunders 1992); *S. b. brunneus* is a new host record.

Rhadinopsylla sp.

We collected 1 female specimen of this flea genus from *S. b. endemicus*. Unfortunately, it could not be identified to species. The locality was Dry Creek Road, Payette Co., 1.4 mi [2.2 km] E Little Willow Creek, T9N, R2W, Sec. 18 [44°07′N, 116°37′W, 815 m elev.], 26 February 1983 (ACMNH 318 [1 f], reported in Baird and Saunders 1992).

The flea is most likely *R. s. sectilis*, which occurs in many western states on deer mice (*Peromyscus* sp.) and ground squirrels, including *S. townsendii* and *S. washingtoni* (Lewis et al. 1988, Baird and Saunders 1992). *Rhadinopsylla* are uncommon fleas and have population peaks in the colder months (Lewis et al. 1988). This is the 1st record of any *Rhadinopsylla* species from *S. brunneus*.

Siphonaptera: Ceratophyllidae

Oropsylla idahoensis (Baker)

This flea species was collected on *S. b. brunneus* at the following locations: Price Valley [45°01′N, 116°26°W, 1270 m elev.], 3 June 1981 (ACMNH 209 [3 f]); and OX Ranch 1–2 km S, 1–2 km E Bear, Adams Co. [45°00′N, 116°39′W, 1340 m elev.] (live-trapping collections).

Oropsylla idahoensis occurs from Alaska to New Mexico and is one of the most common fleas of ground squirrels in the Rocky Mountains and westward. Hosts include other western ground squirrels of subgenus *Spermophilus* (Table 1), golden-mantled ground squirrels (*S. lateralis*), and marmots (*Marmota* sp.; Lewis et al. 1988, Baird and Saunders 1992); *S. b. brunneus* is a new host record.

Oropsylla tuberculata tuberculata (Baker)

This was the most common flea on both *S. b. brunneus* and *S. b. endemicus*, occurring at nearly all locations from which we collected ectoparasites. We found *O. t. tuberculata* on *S. b. brunneus* at the following localities: Price Valley [45°01′N, 116°26°W, 1270 m elev.], 3 June 1981 (ACMNH 209 [1 m], ACMNH 210 [1 m]); Mill Creek summit, 5 km N Hornet Guard Station, Adams Co., T18N, R3W, Sec. 25, 4500′ elev. [44°53′N, 116°39′W, 1370 m], 2 June 1985 (ACMNH 510 [2 m, 3 f], ACMNH 512 [2 m, 3 f]); Lick Creek, Adams Co., T19N, R3W, Sec. 14 [44°54′N, 116°40′W, 1290 m elev.], 17 April 1983 (ACMNH 305 [4 m, 3 f], ACMNH 306 [1 f]); Round Valley, Valley Co. [44°21′N, 116°00′W, 1460 m elev.], 18 May 1985 (ACMNH 315 [1 f]).

Records from *S. b. endemicus* are as follows: Sucker Cr. 11 mi [18 km] N Emmett, Gem Co., T8N, R2W, Sec. 13 [44°02′N, 116°31′W, 830 m elev.], 21 February 1982 (ACMNH 221, 222, 223), 28 February 1982 (ACMNH 225, 226, 227), 3 May 1987 (ACMNH 544 [1 m]); 0.1 mi E Payette Co. line, 12.6 mi [20 km] N Emmett, Gem Co., T8N, R2W, Sec. 12 [44°03′N, 116°32′W, 810 m], 28 February 1982 (ACMNH 224, 236, 237, 238; reported in Baird and Saunders 1992); Dry Creek Road, 1.4 mi [2.2 km] E Little Willow Creek, Payette Co., T4N, R2W, Sec. 18 [44°07′N, 116°37′W, 815 m elev.], 20 February 1983 (ACMNH 318 [10 m, 13 f]), 26 February 1983 (ACMNH 317 [8 m, 3 f]); Weiser Cove, Washington Co. [44°13′N, 116°44′W, 715 m elev.], 7 March 1982

(ACMNH 228, 229, 230); lower Mann Creek, 2.5 mi [4 km] N jct. Weiser River Road, Washington Co. [44°13′N, 116°51′W, 720 m elev.], 14 March 1982 (ACMNH 231, 232, 233, 240, 242, 243, 244); Washington Co., lower Mann Creek, 3.3 mi [5.3 km] N jct. Weiser River Road [44°17′N, 116°51′W, 730 m elev.], 14 March 1982 (ACMNH 239).

This is a very common flea in most of the western United States and western Canadian provinces (Baird and Saunders 1992). Hosts include other western ground squirrels of subgenus *Spermophilus* (Table 1), antelope ground squirrels (*Ammospermophilus leucurus*), woodrats (*Neotoma* sp.), and badgers (Lewis et al. 1988, Baird and Saunders 1992). It was previously recorded from *S. brunneus* by Baird and Saunders (1992).

Thrassis pandorae pandorae Jellison

We found 1 specimen of this flea on *S. b. brunneus* at Lick Creek, Adams Co., T19N, R3W, Sec. 14 [44°54′N, 116°40′W, 1290 m elev.], 17 April 1983 (ACMNH 305 [1 m]).

This flea is distributed from Washington to California and east to Colorado (Stark 1970). It is found most frequently on *Spermophilus armatus*, *S. beldingi*, and *S. elegans* (= *richardsonii* in Stark 1970), but also occurs on *S. columbianus*, *S. elegans* (Table 1), and a variety of other rodents, lagomorphs, and carnivores (Stark 1970). *S. b. brunneus* is a new host record.

Thrassis francisi barnesi Stark

We found this flea on *S. b. endemicus* at Sucker Cr. 11 mi [18 km] N Emmett, Gem Co., T8N, R2W, Sec. 13 [44°02′N, 116°31′W, 830 m elev.], 31 May 1981 (ACMNH 220 [3 m, 4 f]), 3 May 1987 (ACMNH 540 [4 m, 3f], ACMNH 541 [2 m, 1 f], ACMNH 542 [1 m, 6 f], ACMNH 543 [4 m, 7 f], ACMNH 544 [1 m, 1 f], ACMNH 545 [2 m, 1 f], ACMNH 547 [4 m, 9 f], ACMNH 548 [1 f], ACMNH 549 [3 m, 7 f]); 7 mi [11 km] N Emmett, Gem Co., T7N, R1W, Sec. 5 [43°58′N, 116°29′W, 920 m elev], 23 May 1987 (ACMNH 546 [4 m, 2 f]); Sand Hollow, 5.6 km N, 5.0 km E Payette, Payette Co., T9N, R4W, Sec. 7 [44°08′N, 116°51′W, 750 m elev.], 30 March 1989 (USNM 565927 [3 m, 2 f]).

This flea occurs north of the Snake River in western Idaho, and on both sides of the river in eastern Idaho and south into central Utah and eastern Nevada (Stark 1970). Its most common hosts are *S. armatus* and *S. elegans*, rather than *S. townsendii mollis*, the usual host of *T. f. francisi*. Stark (1970) felt that host associations may separate the 2 subspecies of *T. francisi*, although the 2 fleas appeared to intergrade in eastern Nevada. *S. b. endemicus* is a new host record.

Thrassis francisi francisi (Fox)

We collected 14 individuals of this flea from *S. b. endemicus* at 1 locality: Dry Creek Road, 1.4 mi [2.2 km] E Little Willow Creek, Payette Co., T4N, R2W, Sec. 18 [44°07′N, 116°37′W, 815 m elev.], 26 February 1983 (ACMNH 318 [1 m, 5 f], SM2 [2 m, 3 f]), 24 February 1986 (ACMNH 920 [2 m, 1 f]).

This flea is known from the Great Basin desert of eastern Oregon, Idaho south of the Snake River, eastern Nevada, Utah, and parts of Wyoming. It occurs primarily on *S. townsendii*, but the white-tailed prairie dog (*Cynomys leucurus*) is the usual host in Wyoming (Stark 1970). There are incidental records from several species of ground squirrels (Table 1), marmots, and deer mice (Stark 1970). Our records are the 1st from any host north of the Snake River in Idaho (Stark 1970, Lewis et al. 1988, Baird and Saunders 1992); *S. b. endemicus* is a new host record.

Thrassis francisi rockwoodi Hubbard

Two males of this flea were collected from *S. b. endemicus* at a single locality: Sucker Creek, 11 mi [18 km] N Emmett, Gem Co., T8N, R2W, Sec. 13 [44°02′N, 116°31′W, 830 m elev.], 21 February 1982 (ACMNH 223), 28 February 1982 (ACMNH 227 [2 m]; reported in Baird and Saunders 1992).

This subspecies has been recorded from eastern Oregon, northwestern Nevada, and northern California, where it occurs most commonly on *S. beldingi*, although collections have been made from *S. townsendii* (Stark 1970, Lewis et al. 1988).

Acarina: Ixodidae

Ixodes sculptus Neumann

We collected specimens of this tick from *S. b. brunneus* at 1 locality: OX Ranch 1–2 km S, 1–2 km E Bear, Adams Co. [45°00′N, 116°39′W, 1340 m elev.] (live-trapping collections).

This widespread tick occurs from western Canada south to California and Texas and east across the Great Plains. It occurs on several western ground squirrels of the subgenus *Spermophilus* (Table 1), prairie dogs (*Cynomys* sp.), marmots, voles (*Microtus* sp.), pikas (*Ochotona* sp.), gophers (*Thomomys* sp.), jumping mice (*Zapus* sp.), domestic animals, and various carnivores (Doss et al. 1974). *S. b. brunneus* is a new host record.

Acarina: Laelapidae

Androlaelaps fahrenholzi (Berlese)

We collected 8 specimens of this mite from *S. b. endemicus* at the following localities: Sucker Cr. 11 mi [18 km] N Emmett, Gem Co., T8N, R2W, Sec. 13 [44°02′N, 116°31′W, 830 m elev.], 21 February 1982 (ACMNH 227 [4 f, 2 deutonymphs]); lower Mann Creek, 2.5 mi [4 km] N jct. Weiser River Road, Washington Co. [44°16′N, 116°51°W, 720 m elev.], 14 March 1982 (ACMNH 233 [2 f]).

This mite is widespread in Eurasia, North America (Whitaker 1979), and Central America (Strandtmann 1949). It occurs on a wide variety of mammals, including marsupials (*Didelphis* sp.), insectivores, bats, several families of rodents, lagomorphs, carnivores, and birds (Strandtmann 1949, Whitaker and Wilson 1974, Rayburn et al. 1975). Opossums, insectivores, and rodents are the primary hosts, but *A. fahrenholzi* has the least host specificity and widest geographic range of any North American ectoparasitic mite (Whitaker 1979). These are the 1st records from *S. brunneus*.

Nematoda: Rhabditidae

Rhabditis (*Pelodera*) *orbitalis* Sudhaus and Schulte

We observed this parasitic eyeworm only in live-trapped *S. b. brunneus* from OX Ranch 1–2 km S, 1–2 km E Bear, Adams Co. [45°00′N, 116°39′W, 1340 m elev.].

All specimens were collected in April and May 1990 to 1994. We found them in 1 eye or both eyes of yearling and adult *S. b. brunneus*. The number per eye varied from 0 to 1272. The museum specimens were not checked for eyeworms. In 1994, T. A. Gavin and P. W. Sherman examined 21 live-trapped *S. b. endemicus* from Sand Hollow, Payette Co., and found no eyeworms.

This eyeworm has been reported previously from Eurasian and North American voles and lemmings (*Microtus* spp., *Lemmus trimucronatus*, *Dicrostonyx groenlandicus*, *Pitimys subterraneus*, *Arvicola terrestris*, and *Clethrionomys* spp.), mice (*Apodemus* spp. and *Mus musculus*), and rats (*Rattus norvegicus*; Poinar 1965, Kinsella 1967, Cliff et al. 1978, Hominick and Aston 1981, Schulte 1989). *S. b. brunneus* is a new host record, the 1st record of any *Rhabditis* from Sciuridae, and also the 1st record of *R. orbitalis* from Idaho.

Epizootics

In 11 field seasons (April–June) of work with *S. b. brunneus*, we found only 2 dead individuals, and none were observed sick or dying. While a number of populations have declined (T. A. Gavin, P. W. Sherman, and E. Yensen personal observation), mortality occurred while the animals were in hibernation rather than during the active season. The most serious population declines were estimated to be around 50% in 1 yr, rather than the 95%–100% active season mortality typically associated with plague (Lechleitner et al. 1968, Rayor 1985). Although numbers of fleas on individual squirrels were relatively low, especially in *S. b. brunneus*, all flea species we collected are important in plague epidemiology in other hosts (Pratt and Stark 1973) and could potentially play a role in an Idaho epizootic.

DISCUSSION

Collections of ectoparasites from *S. brunneus* have resulted in new state records for the flea *Thrassis francisi rockwoodi* and the eyeworm *Rhabditis orbitalis*, plus 9 new host records. Because there have been no previous studies of *S. brunneus*, the new records are hardly surprising. However, the records of *Thrassis f. francisi* and *T. f. rockwoodi* on *S. b. endemicus* were unexpected. *Thrassis f. barnesi* occurs north of the Snake River in the Snake River Plain (Stark 1970) and is the subspecies of *Thrassis francisi* that would be expected to occur in the range of *S. b. endemicus*. Instead, we found *Thrassis f. francisi*, which is common in *S. townsendii mollis* south of the Snake River, and *T. f. rockwoodi*, for which the nearest locality is from Oregon across the Snake River (Stark 1970), a major biogeographic barrier in southern Idaho (Davis 1939). This interesting situation merits further study.

With the exception of eyeworms, ectoparasites of *S. brunneus* are all known from multiple other species of ground squirrels (Table 1). Thus it is curious that *S. b. brunneus* and *S. b.*

endemicus shared only a single ectoparasite, *Oropsylla t. tuberculata*, a widespread flea found on at least 4 other species of ground squirrels. By contrast, the geographically and taxonomically close (Nadler et al. 1984) *S. townsendii* has all but one of the ectoparasite species found on both *S. brunneus* subspecies. However, *Spermophilus townsendii* is now recognized (Hoffmann et al. 1993) as a complex of 3 closely related sibling species with different karyotypes, and it was not always clear to us from the literature (Table 1) which parasites were associated with which host. Consequently, we have treated *S. townsendii* as a single entity herein.

There are several possible explanations for the lack of shared ectoparasites between *S. b. brunneus* and *S. b. endemicus*: (1) they are geographically separated, and their ranges are inhabited by different ectoparasites; (2) they occur in different habitats and therefore have different ectoparasites; (3) pelage differences between them may be different "microhabitats" for ectoparasites; (4) possibly the formerly shared ectoparasites on one or the other subspecies have been lost via a founder event, due to population structure, or because of population bottlenecks; and (5) we did not adequately sample all ectoparasites on either subspecies. Among these hypotheses, (5) is the least interesting evolutionarily, and (4) is the most interesting.

Most western ground squirrel species are allopatric or parapatric; thus, there is little possibility of direct transmission of ectoparasites among them. Historically, the 2 subspecies of *S. brunneus* were separated by 19 km, 250 m in elevation, and a habitat change from arid shrub-steppe vegetation to montane meadows (Yensen 1991). At present, the nearest extant populations are separated by 48 km. Because *S. townsendii* is allopatric to *S. brunneus*, occurs in nonmontane habitats, and has all ectoparasites found on both subspecies of *S. brunneus*, differences in geography (hypothesis 1) and habitats (2) are unlikely to be the sole explanations for the differences in ectoparasites between *S. b. brunneus* and *S. b. endemicus*.

There are significant differences in pelage length between *S. b. brunneus* and *S. b. endemicus* (Yensen 1991). Interestingly, the pelage of *S. townsendii* is intermediate in length between the 2 *S. brunneus* subspecies (E. Yensen unpublished data). There also appear to be differences in hair density and diameter, although these were not quantified by Yensen (1991). Possibly *S. townsendii* is inhabitable by the entire set of ectoparasites, and each subspecies of *S. brunneus* is a suitable host for about half the set. Thus, pelage differences (hypothesis 3) are a possible explanation for the lack of overlap in ectoparasite species between 2 very close relatives, but it would not explain the differences in parasite loads or the low percentages of nonparasitized individuals.

Anderson and May (1979) argued that parasite infestations should be sensitive to host population structure (hypothesis 4). As population size declines and populations become more isolated, the probability of parasite species loss should increase. Our data were consistent with this pattern: the proportion of parasitized *S. b. brunneus* was significantly lower than that of *S. b. endemicus*; the former has smaller, more isolated populations.

The isolated *S. b. brunneus* populations would also retard exchange of ectoparasites among populations. Thus, there might be stochastic losses of parasite populations with low probability of recolonization (Anderson and May 1979). The differences in incidence of parasites between *S. b. brunneus* and *S. b. endemicus* are consistent with this interpretation.

The low density and wide dispersion of individuals within *S. b. brunneus* populations at a site (E. Yensen and P. W. Sherman personal observation) may also retard direct transfer of ectoparasites, and, consequently, *S. b. brunneus* populations may not be able to support large ectoparasite populations. The low incidence of parasitism in Idaho ground squirrels thus appears to be related to population structure.

Because we did not examine ground squirrels under a microscope, we do not suppose that all ectoparasites were collected (hypothesis 5). However, there was no systematic bias in the sampling that would account for the differences in the proportion of parasitized animals and parasite load differences between *S. b. brunneus* and *S. b. endemicus*. The low proportion of parasitized *S. b. brunneus* (28%) and *S. b. endemicus* (70%) in this study may have been partially because our collecting techniques missed smaller ectoparasites. However, the same techniques were used for both subspecies; therefore, the sampling differences between them should reflect real differences in parasite load. Thus, with the number of animals and localities sampled, the low overlap in lists of parasites is striking.

Further, the low proportion of *S. brunneus* with ectoparasites (55%), especially in *S. b. brunneus*, is atypical of *Spermophilus*. For example, Hilton and Mahrt (1971) found that in Alberta 100% of *S. columbianus* and *S. franklinii* and 92% of *S. richardsonii* had ectoparasites. We were collecting *S. townsendii* and *S. columbianus* at the same time as *S. brunneus* and were impressed by the much higher parasite loads on those species.

Although we did not observe plague in *S. brunneus* during this study, it does occur in southwestern Idaho. Serum samples positive for *Yersina pestis*, the plague bacterium, were reported from *S. townsendii* during a major ground squirrel die-off in 1941–42 in Ada, Canyon, and Payette counties, immediately south of the range of *S. b. brunneus* (Hubbard 1947, Link 1955). In 1975–1977, positive antibody titers to plague were found in 72%–91% of badgers in the Snake River Birds of Prey Area, 50 km south of the range of *S. b. endemicus* (Messick et al. 1983). Badgers are important predators of ground squirrels. Eight of 9 dead Townsend's ground squirrels examined by Messick et al. (1983) were positive for *Y. pestis*. The plague bacterium has been detected in other species of *Spermophilus* in all 5 Idaho counties where *S. brunneus* populations exist, but until 1995 no *S. brunneus* had been examined (Idaho Department of Health and Welfare personal observation). In April 1995, T. A. Gavin found a dead *S. b. brunneus* at the OX Ranch and sent it to the Wyoming State Veterinary Laboratory (Laramie) where it was assigned case #95W3914. The carcass was found to be negative for *Y. pestis* (E. Williams personal comment). Nonetheless, in the event of a plague epizootic, local populations of *S. brunneus* could easily be decimated. With only a small number of populations remaining, plague could jeopardize the survival of both subspecies of *S. brunneus*.

NOTE ADDED IN PRESS

Six hibernacula of *S. b. brunneus* were excavated in spring 1995 (Yensen and Sherman unpublished data). Nests recovered from the hibernacula were placed in plastic bags in the field, taken to the laboratory, and then placed in Berlese funnels; small invertebrates were collected in 70% ethanol. Only the fleas have been identified to date, but we can now add the following records:

Neopsylla inopina

Adams Co., 1.5 km N, 1.5 km E Bear Guard Station, 28 April 1995 [6 m, 7 f]; Adams Co., Steve's Creek, 2 km S, 2 km E Bear, 15 April 1995 [8 m, 7 f]; Adams Co., mouth of Cold Springs Creek, 14 May 1995 [1 m, 1 f].

Oropsylla idahoensis

Adams Co., 1.5 km N, 1.5 km E Bear Guard Station, 28 April 1995 [1 m, 2 f]; Adams Co., Steve's Creek, 2 km S, 2 km E Bear, 15 April 1995 [4 m, 2 f]; Adams Co., 3 km S Bear, 16 April 1995 [1 f].

Oropsylla tuberculata tuberculata

Adams Co., 1.5 km N, 1.5 km E Bear Guard Station, 28 April 1995 [18 m, 16 f]; Adams Co., Steve's Creek, 2 km S, 2 km E Bear, 15 April 1995 [20 m, 21 f]; Adams Co., mouth of Cold Springs Creek, 14 May 1995 [3 f].

Thrassis pandorae pandorae

Adams Co., 1.5 km N, 1.5 km E Bear Guard Station, 28 April 1995 [28 m, 31 f]; Adams Co., Steve's Creek, 2 km S, 2 km E Bear, 15 April 1995 [8 m, 15 f]; Adams Co., 3 km S Bear, 16 April 1995 [1 m].

Catallagia sp., prob. *descipiens*

Adams Co., 1.5 km N, 1.5 km E Bear Guard Station, 28 April 1995 [1 f].

Foxella ignota

Adams Co., Steve's Creek, 2 km S, 2 km E Bear, 15 April 1995 [4 m, 3 f].

Spermophilus b. brunneus is a new host record for *Catallagia* sp. and *Foxella ignota*. *Catallagia decipiens* is widely distributed in the western United States and is usually found on deer mice (Baird and Saunders 1992). *Foxella ignota* is commonly found on pocket gophers in the northern Rocky Mountains (Hubbard 1947).

These new records also indicate that different sets of ectoparasites occur on *S. b. brunneus* and *S. b. endemicus*, thus corroborating the earlier results. The same 4 flea species were again found associated with *S. b. brunneus*, and neither *Catallagia* nor *Foxella* is known from *S. b. endemicus*.

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ROOST SITES OF THE SILVER-HAIRED BAT (*LASIONYCTERIS NOCTIVAGANS*) IN THE BLACK HILLS, SOUTH DAKOTA

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ABSTRACT.—We investigated the roosting ecology of silver-haired bats (*Lasionycteris noctivagans*) in the Black Hills of western South Dakota. Using radiotelemetry, we located 39 roosts, 10 of which were maternity aggregations containing 6 to 55 bats. The roosts were mostly in ponderosa pine (*Pinus ponderosa*) snags that averaged 39 cm diameter at breast height. Solitary bats preferred roosting under loose bark or in crevices in trees, regularly moving among trees. All maternity aggregations were found in tree cavities, primarily those created by woodpeckers. Roost trees were located in patches of forest with relatively high snag densities, about 21 snags/ha. This study suggests that snags play an important role in maintaining silver-haired bat populations in ponderosa pine ecosystems.

Key words: Lasionycteris noctivagans, *silver-haired bat, roosts, snags.*

The silver-haired bat (*Lasionycteris noctivagans*) occurs widely across North America at highly variable densities (Barbour and Davis 1969, Kunz 1982a). Studies conducted in the northwestern United States suggest that silver-haired bats occur more frequently in late-successional forests dominated by trees over 200 yr old than in early seres (Perkins and Cross 1988, Thomas 1988). This association is attributed to the presence of high concentrations of standing dead trees, some of which have exfoliating bark, cracks in the wood, and cavities excavated by birds—sites that may be preferred by bats for roosting (Perkins and Cross 1988, Thomas 1988, Campbell et al. in press). Little information on summer roost sites for silver-haired bats is available (Kunz 1982a), particularly in areas that lack abundant stands of late-successional forests. Barclay et al. (1988) searched trees in Manitoba and found silver-haired bats roosting under folds of loose bark during the migration period. Parsons et al. (1986) reported observations of 2 small silver-haired bat maternity colonies in hollow trees in Canada. Likewise, maternity colonies have been found in cavities of both live and dead trees in California (Rainey et al. in press). Despite these records, a clear understanding of silver-haired bat roosts and roost habitat is still lacking.

To better understand the roost requirements of silver-haired bats, we investigated roost selection by the silver-haired bat in the Black Hills of South Dakota. Although forests in this region have been intensively managed for timber (Boldt and Van Deusen 1974), silver-haired bats are relatively abundant compared to the 9 other bat species present in the region (Mattson 1994). Although Mattson (1994) captured twice as many males as females, pregnant or lactating females were not uncommon. Our goal was to characterize roost selection by silver-haired bats in terms of attributes potentially affected by current forestry practices.

STUDY AREA

Our study area is located in the southern Black Hills of South Dakota near the town of Custer (43°46′N, 103°35′W). Most of the study area is in the Black Hills National Forest and occurs at elevations from 1360 to 1985 m asl. The topography of the area varies from rolling highlands with parklike valleys to narrow, steep canyons with rocky ridge tops. The climate of the Black Hills differs from the surrounding semiarid plains in that it is moister and less subject to temperature extremes. Average maximum temperature at Custer in July is about 23° C, while mean annual precipitation is 457 mm.

The forests of the area are dominated by pure stands of ponderosa pine (*Pinus ponderosa*). Small stands of quaking aspen (*Populus tremuloides*) precede ponderosa pine on disturbed sites. Paper birch (*Betula papyrifera*) grows in small clusters in more mesic sites, whereas

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Rocky Mountain juniper (*Juniperus scopulorum*) grows on dry ridges.

The forests of the Black Hills have been managed for timber production since logging first began in the 1870s. During the past 100 yr, most areas have been cut once, and many have experienced multiple partial cuts (Alexander 1987). In all, nearly 12 × 10^6 m^3 of timber has been removed. Only a few small scattered stands of unharvested forest remain (Boldt and Van Deusen 1974). Although clearcutting was once the primary means of harvest, shelterwood cutting, a method using a series of cuts, is now standard.

We delineated two 10.1 × 10.1-km study sites in areas in which we located silver-haired bat roosts. The Jewel Cave Study Site encompasses Jewel Cave National Monument and adjacent areas of the Black Hills National Forest. The Hazelrodt Study Site is located southeast of Custer on national forest land and Custer State Park. Much of the Hazelrodt Study Site burned during a fire in 1990 that covered over 5670 ha.

MATERIALS AND METHODS

Capture and Tracking Techniques

Silver-haired bats were captured using mist nets set above small ponds and streams between 25 June and 4 August 1994. We determined the sex and reproductive condition for all captured bats using external features (Racey 1988). Bats were classified as adult or juvenile based on fusion of the epiphyseal-diaphyseal suture of the finger bones (Anthony 1988).

We attached 0.7-g radio transmitters (model BD-2B, Holohil Systems Ltd., Woodlawn, Ontario) to 4 adult males and 12 adult females. After fur had been trimmed from the bats, transmitters were attached to the area between the shoulder blades using a cyanoacrylate-based glue (Fing'rs, Camarillo, CA). Bats to which transmitters were affixed weighed 11–14 g, so that transmitters represented 5–6.4% of body mass, slightly over the 5% maximum recommended by Aldridge and Brigham (1988). We did not use any other marking technique to identify individuals.

Hand-held, 3-element yagi antennas and portable receivers (model TR-2, Telonics, Mesa, AZ) were used to track bats to roost trees. If we were unable to determine where in the tree the bat was roosting, or whether it was alone or with others, we returned to the tree before dusk to watch and count bats leaving the site. We attempted to approach the tree quietly to reduce disturbance. We used a bat detector (Bat Box III, Stag Electronics, St. Agnes, England) to listen for echolocation calls. These, along with body size and flight pattern, were used to confirm that bats in a given roost were only silver-haired bats.

Roost Measurements

We located 18 roost trees in the Jewel Cave Study Site and 21 in the Hazelrodt Study Site. When possible, the type of roost (i.e., woodpecker cavity, crevice, loose bark, etc.) was recorded. Each roost tree was classified as being used by either a maternity aggregation or solitary bats. Maternity roosts, located by tracking pregnant and lactating females, always contained 6 or more bats. Solitary roosts contained only a single bat and were located by tracking males or females that did not appear pregnant or lactating or were post-lactating. We categorized the aspect of the roost exit as northeast (0–89°), southeast (90–179°), southwest (180–269°), or northwest (270–359°).

Each roost tree was identified to species and its height and diameter at breast height (dbh) measured. We placed each roost tree into 1 of 7 decay stages; decay stage 1 included live trees with intact bark and branches, whereas decay stage 7 included dead trees beginning to decompose with broken tops and no loose bark (Thomas et al. 1979).

Plot Measurements

Within a 5-m-radius (78-m^2) circular plot centered at each roost tree, we measured average tree size, total basal area, and snag density. Trees were defined as standing woody stems >1.5 m in height and >10 cm dbh. We also recorded whether disturbance by fire or logging had taken place in each plot. Disturbance by fire was considered to have occurred if there was any charred woody material in the plot, and disturbance by logging was noted if we observed any saw cuts on woody material in the plot.

To compare characteristics of roost site plots with the surrounding areas, we located four 5-m-radius neighborhood plots for each roost plot and recorded the same information as for roost plots. We located the center of the neighborhood plots by pacing 100 m from the roost tree in each of the cardinal directions (north, south, east, west) and then pacing an additional 30 m in a randomly selected direction.

We measured elevation and distance to the nearest source of water for each roost tree using topographic maps (7.5 minute series, USGS, Denver, CO). For comparison, we randomly located a point in the Jewel Cave Study Site or Hazelrodt Study Site for each roost tree found in that site. To examine roost site selection on a larger scale, we calculated the number of snags in all neighborhood plots to estimate snag density for the study site generally. This estimation was made by dividing the total number of snags in the 156 neighborhood plots by their total area. The fire in the Hazelrodt Study Site inflated snag densities in this area. To remove the influence of fire, we calculated snag densities within the study sites by removing the 77 neighborhood plots that had been disturbed by fire.

Analysis

Chi-square tests for goodness-of-fit (Jelinski 1991) were used to compare observed with expected roost aspects and tree decay stages by roost type (maternity vs. solitary). For the latter test, because of small sample size, we pooled the roost trees into 3 decay stage categories: stage 1–3, stage 4, and stage 5–7.

To compare continuous attributes between roost plots and neighborhood plots, we subtracted attribute means for the 4 neighborhood plots from corresponding means for the roost plots. So, each roost plot was compared only to its 4 neighborhood plots. We tested the null hypotheses that the mean differences did not differ from 0 using paired t tests. Chi-square tests for homogeneity (Jelinski 1991) were used to compare observed with expected disturbances at roost plots. Expected disturbances were based on the proportion of neighborhood plots that had burned or been logged. We used 2-sample t tests to compare the means for elevation and distance to nearest water for roost sites and random sites. To avoid type 1 errors that may result from using a number of inferential statistical tests with the same predictor variable, we arbitrarily set $\alpha = 0.025$.

RESULTS

Roost Attributes

We radio-tracked 16 bats for a mean of 8 d (range: 1–20) and located 39 roosts, all of which occurred in trees. Nine adult females were tracked to 10 trees that were used by maternity aggregations averaging 22.2 ± 4.9 ($s_{\bar{x}}$) individuals (range: 6–55). Three other females and 4 adult males were tracked to 25 roost trees, none of which were used by maternity aggregations. Three of the females that originally used maternity aggregations were later followed to 4 trees where they roosted alone. Maternity roosts were found exclusively in tree cavities, primarily those created by woodpeckers (Picidae). Cavity openings were 7.5–10 cm in diameter. Solitary bats roosted under loose bark ($n = 15$), in a tree crack or crevice ($n = 5$), or in a woodpecker cavity ($n = 1$). We could not determine the specific roost location for 8 trees. These trees were placed in the solitary category because bats tracked to these 8 trees were always observed roosting alone at other trees. Maternity roosts were 10.2 ± 1.5 m (range: 3.1–13.8) aboveground. The height of measured solitary roosts averaged 3.4 ± 0.5 m (range: 0.9–8.9). Cavity openings of maternity roosts and solitary bat roosts were found more frequently on the south side of tree boles over other aspects ($\chi^2 = 15.8$, d.f. = 3, $P = 0.001$).

Of 39 roost trees, 38 (97%) were ponderosa pine and 1 (3%) was aspen. Of 508 trees on neighborhood plots, 483 (95%) were ponderosa pine and 25 (5%) were other species: aspen, juniper, and paper birch. The 10 trees used by maternity aggregations of silver-haired bats ranged from decay stage 2 to 7 (median = 5). The 29 trees used by solitary bats varied from tree decay stage 3 to 7 (median = 4). Trees in neighborhood plots ranged from decay stage 1 to 7 (median = 1). Bats in maternity aggregations selected roost trees in significantly different decay stages than solitary roosting bats ($\chi^2 = 10.2$, d.f. = 2, $P = 0.0062$; Fig. 1). Roost trees averaged 14.2 ± 0.9 m (range: 3.7–24.1) in total height, and 39 ± 2 cm dbh (range: 13–63). They averaged 17 ± 2 cm larger in dbh than neighborhood trees. The 10 maternity roost trees averaged 44 ± 4 cm dbh (range: 29–62), 24 ± 4 cm larger than neighborhood trees. The 29 solitary roost trees averaged 37 ± 2 cm dbh (range: 12–55), 15 ± 3 cm larger than neighborhood trees. Maternity and solitary roost trees did not differ in diameter ($t = 1.64$, $P = 0.12$).

The 9 bats found in maternity aggregations returned to the same roost tree for a mean of 8 d (range: 1–21). We tracked 1 bat from a tree containing a maternity aggregation of 55 bats

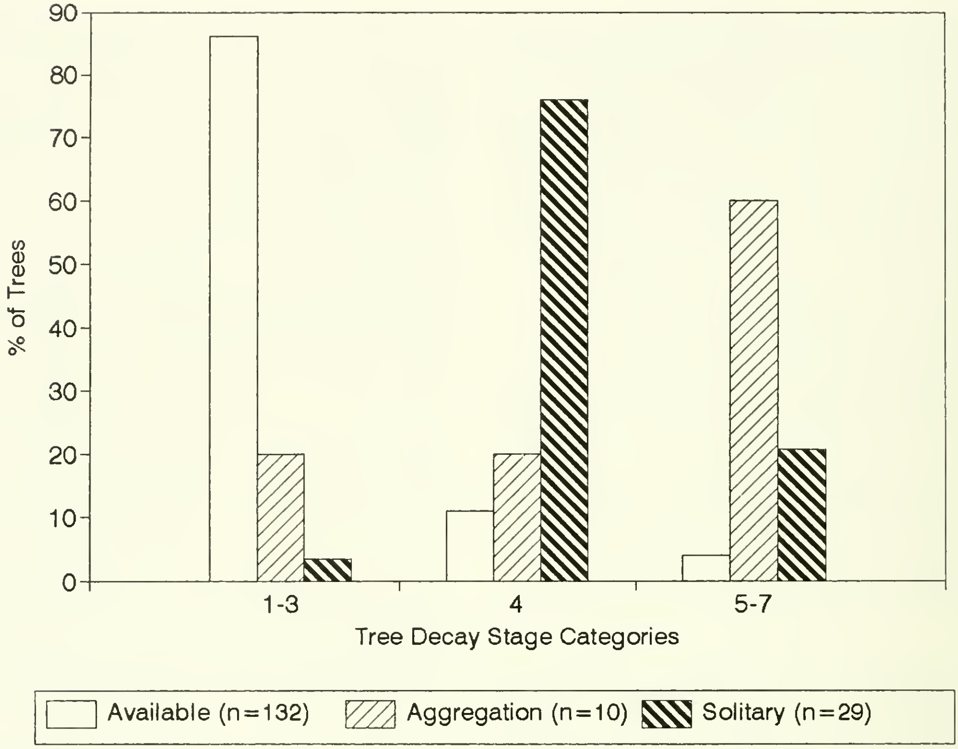

Fig. 1. Percentages of trees in each tree decay stage category used by maternity aggregations and solitary roosting silver-haired bats, and available trees in the Black Hills, South Dakota, June–August 1994.

to a 2nd tree with a maternity aggregation of 44 bats about 440 m away. The following evening no bats were observed exiting from the 1st roost tree, but it is not clear how many bats from the 1st roost tree moved to the 2nd tree with the bat we were tracking.

We tracked 10 bats that used solitary roosts to a mean of 3 solitary roost trees (range: 1–6). For the most part, these bats switched trees daily. However, on 5 occasions solitary bats used the same tree on consecutive days. Three of the 7 solitary roosting bats that we followed to multiple trees returned at least once to trees they had used several days before. Solitary roosting bats traveled a mean of 405 ± 93.7 m ($n = 13$) between successive roost trees. Radio-tracked bats traveled a mean of 2060 ± 440 m ($n = 12$) from the capture point to their first roost tree, significantly farther ($t = 3.67$, $P = 0.004$) than the distance between successive roost trees.

Plot Attributes

Roost plots had 1.7 ± 0.6 more live trees ($t = 3.09$, $P = 0.004$) than neighborhood plots. Live and dead trees on roost plots were 6.5 ± 1.7 cm larger in dbh on average than those on neighborhood plots ($t = 3.77$, $P = 0.0006$). Roost plots also had basal areas of both live and dead standing trees that were 14.07 ± 3.46 cm^2/m^2 greater ($t = 4.06$, $P = 0.0002$) than neighborhood plots. Neither fire disturbance ($\chi^2 = 0.005$, d.f. = 1, $P = 0.94$) nor logging disturbance ($\chi^2 = 2.72$, d.f. = 1, $P = 0.099$) differed between roost and neighborhood plots. Maternity and solitary plots did not differ in the attributes studied (Table 1). Roost trees tended to be located higher in elevation than random points ($t = 1.67$, $P = 0.10$). Roost sites were significantly farther from water than random points ($t = 2.78$, $P = 0.007$).

Using all 156 neighborhood plots, we calculated snag density for the area to be 117 snags/ha. After removing 77 neighborhood plots that were disturbed by fire, we recalculated snag densities to be 21 snags/ha.

DISCUSSION

Roosts used by maternity aggregations differed from those used by solitary silver-haired

TABLE 1. Comparison between solitary and maternity roost plot attributes in the Black Hills, South Dakota, June–August 1994.

Attribute	Solitary ($n = 29$)	Maternity ($n = 10$)	T	P value
Live trees (no./plot)	4.5 ± 0.6	5.2 ± 0.7	0.72	0.47
Snags (no./plot)	2.1 ± 0.5	2.2 ± 0.5	0.15	0.88
Mean tree dbh (cm)	26.7 ± 3.2	27.5 ± 1.9	0.22	0.83
Total basal area (cm^2/m^2)	17.8 ± 1.3	25.3 ± 4.7	1.54	0.13

bats. Maternity aggregations always used a hollow cavity within a tree bole. Usually these cavities were created by woodpeckers, likely hairy woodpeckers (*Picoides villosus*) or black-backed woodpeckers (*P. arcticus*), based on the size of the openings (Terres 1980). Although rare in the Black Hills (Black Hills National Forest 1989), Lewis' woodpeckers (*Melanerpes lewis*), northern flickers (*Colaptes auratus*), or three-toed woodpeckers (*Picoides tridactylus*) may have excavated some of the cavities. Solitary roosts were located under loose bark or in a natural crack or crevice in the tree bole. Only once did a solitary bat use a woodpecker cavity. Although silver-haired bats are cryptically colored, they were never observed roosting openly on a tree trunk or limb, or in foliage. This behavior differs from other cryptically colored, tree-roosting bats (e.g., *Lasiurus* spp.), which tend to roost among tree foliage (Shump and Shump 1982a, 1982b). Roosts required by maternity aggregations may limit silver-haired bat abundance; clearly trees with cavities are less available than are those without. Reproductive females seem to require roosts that provide a relatively enclosed and unexposed space for protecting young from predators or maintaining the necessary thermal environment.

Cavity openings of maternity roosts and solitary bat roosts occurred more frequently than expected on the south side of tree boles. We hypothesize that these roosts are warmer than sites facing north because of insolation and that these differences result in energetic savings, providing more energy for growth and development (McNab 1982). Reller (1972) has shown that several species of woodpeckers orient their nest cavity openings southwesterly for warming by the sun and/or ventilation by the wind. However, it is unclear whether bat use of cavities with south-facing entrances reflects the selections of bats or woodpeckers.

Silver-haired bats roosted exclusively in trees during the summer. Although all but one of the roosts were located in ponderosa pine trees, the dominance of ponderosa pine in our study area prevented us from testing for tree species preference. The wide geographic distribution of silver-haired bats relative to that of ponderosa pine and the use by silver-haired bats of both coniferous and deciduous roost trees in other parts of their range (Novakowski 1956, Parsons et al. 1986, Barclay et al. 1988, Campbell et al. in press, Rainey et al. in press) suggest that these bats select for the structure of the roost itself rather than for a particular tree species. As for other tree-roosting bats (Tidemann and Flavel 1987), it is unlikely that tree species is important to silver-haired bats except that at the local level 1 species may tend to have preferred attributes.

Roost trees were standing, dead, and larger than average in diameter. The single living tree selected as a roost was dying (stage 2) and missing its top; it also had many dead limbs and several woodpecker holes high in the bole. There was an observed difference in tree decay stage between roost trees used by maternity aggregations and solitary bats. Solitary roosting bats frequently used trees in decay stage 4, which are characterized by the presence of loose bark. Alternatively, maternity roosts tended to be found in older, more decomposed trees (decay stages 5–7), trees that are more commonly used by excavating woodpeckers (Thomas et al. 1979). Although the importance of snags as roost sites in other forest types remains in question, large snags appear to be important resources for silver-haired bats in ponderosa pine forests.

Clearly, solitary roosting silver-haired bats switch roosts regularly. This lack of fidelity may be related to the abundant nature of potential roosts (Brigham 1991) or a predator-avoidance strategy (Kunz 1982b). Because they will return to roost trees used several days previously and these roosts are often close together, solitary bats may use a series of trees in the same area and thus maintain a level of site familiarity. Conversely, maternity aggregations tend to remain in the same roosts for longer periods. This may be related to the less abundant nature of tree cavities and the importance of retaining roosts that are suitable for raising offspring. At least some of the maternity aggregations appear to switch roosts during the reproductive period. The reason for this is not clear, although it may involve predator or ectoparasite avoidance (Lewis 1995).

We expected bats to select roosts relatively close to water bodies, minimizing energetic costs of moving between roosting areas and areas potentially used for drinking and foraging. Although trees were abundant in the study sites, bats traveled an average of >2 km from point of capture to their 1st roost tree, and significantly farther from water than expected randomly. This seems to support other available evidence for insectivorous bats in that roost site location is not strongly influenced by commuting costs (Fenton et al. 1985, Brigham 1991). Roost sites located farther from water than random points appear puzzling but may represent the large number of roost trees located along hill or ridge tops, sites with potentially higher snag densities.

Silver-haired bat roost trees were found at sites that differed from nearby areas in a number of attributes. Roost plots differed in having more, large trees and hence a higher total basal area than surrounding plots. Roost trees located in areas that are ideal for tree growth or are logged infrequently might explain why the roost plots have more, larger trees.

Undoubtedly, snags are important in providing roost sites for silver-haired bats in the Black Hills. As suitable roosts are critical resources for bat survival (Kunz 1982b), snag availability likely influences the distribution and abundance of this species. Forest stands containing silver-haired bat roosts had snag densities of 21 snags/ha, a value much higher than current management objectives. These densities were even higher in the Hazelrodt Study Site, an area with a large number of fire-killed trees. How fire suppression and logging practices have affected the number of snags in the Black Hills remains unclear; however, early photographs suggest that many forested areas were more open with many standing dead trees (Knight 1994). Because snags are used for nests or roosts by a large number of vertebrate species (Thomas et al. 1979), reduced snag densities may increase interspecific competition. We hypothesize that forest management practices that reduce snag densities will lead to declines in local silver-haired bat populations.

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PERCEPTIONS OF UTAH ALFALFA GROWERS ABOUT WILDLIFE DAMAGE TO THEIR HAY CROPS: IMPLICATIONS FOR MANAGING WILDLIFE ON PRIVATE LAND

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ABSTRACT.—We conducted a survey of Utah alfalfa (*Medicago sativa*) growers in 1993 to identify wildlife damage problems to hay crops. Such surveys can provide wildlife managers with important insights regarding landowners' wildlife damage management concerns and needs. Pocket gophers (*Thomomys* spp.) and mule deer (*Odecoileus hemionus*) were perceived by growers as causing the most damage. Respondents reported a total annual loss of $350,000 or $24.79/ha (2.8% of the total crop value) because of wildlife damage in alfalfa crops. Decreased hay quantity was the most frequently cited problem caused by wildlife. Compensation and incentive programs were preferred over assistance and information programs for managing wildlife damage in alfalfa crops.

Key words: wildlife damage perceptions, alfalfa growers, wildlife damage management, wildlife management.

Alfalfa is an important livestock forage. In 1994 over 58 million tons of alfalfa hay were harvested in the U.S. on 9,802,400 ha of privately owned land. This represents over 40% of the hay harvested as livestock forage (National Agricultural Statistics Service 1995).

Alfalfa hay is the most important cash crop grown in Utah. In 1994 Utah farmers harvested 2,205,000 tons of alfalfa on 210,000 ha of privately owned land. This crop was worth $158 million (Gneiting 1994).

Rodents, lagomorphs, ungulates, and waterfowl can impact alfalfa production (Piper 1909, Sauer 1978, Luce et al. 1981, Dunn et al. 1982, Packam and Connolly 1992, Austin and Urness 1993, Conover 1994). Big game grazing of alfalfa during the growing season creates conflicts between growers and wildlife managers (Austin and Urness 1993).

Conflicts also may arise between landowners and wildlife managers because of differing perceptions about the extent of wildlife damage in cultivated crops. Farmers may feel that wildlife managers are unaware of the extent of crop losses caused by wildlife and hence are insensitive to their needs (Decker et al. 1984, Conover and Decker 1991). Crop owners' concerns about wildlife damage strongly affect how the agricultural community will respond to environmental issues and whether federal or state wildlife programs aimed at maintaining or improving wildlife habitat on private property will succeed (Conover 1994).

There is consensus among professionals working for federal and state wildlife and agricultural agencies that wildlife damage reduces the profitability of U.S. agriculture (Conover and Decker 1991). Professionals agree that wildlife depredation has increased over time but disagree over the seriousness of the impact. Although the actual costs associated with wildlife depredation are difficult to estimate and can differ on each farm or ranch and crop type (Tebaldi and Anderson 1982, Austin and Urness 1987a, 1987b, 1989, 1993, Lewis and O'Brien 1990), landowners have demonstrated an ability to accurately assess crop losses caused by wildlife (Decker et al. 1984, Conover 1994, McIvor and Conover 1994a). Crop losses and potential future losses caused by, or related to, the presence of wildlife must be assessed to determine if control is warranted (Rennison and Buckle 1988).

Several Great Basin states including Utah, Wyoming, Colorado, New Mexico, Nevada, Idaho, and Arizona have enacted laws to compensate crop owners for wildlife-caused damage (Musgrave and Stein 1993). These actions have been initiated largely in response to constituent concerns over the economic impact of depredating wildlife, particularly big game, in cultivated crops.

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Crop owners in Utah may destroy depredating big game animals if the animals are not removed by the Utah Division of Wildlife Resources (UDWR) within 72 h of notification (Chapter 183, Utah Code 1993a). Utah crop owners also may receive monetary compensation for damage caused by big game animals (Chapter 307, Utah Code 1994b) and ring-necked pheasants (*Phasianus colchicus*; Chapter 46, Utah Code 1971).

We surveyed Utah alfalfa growers to determine their perceptions regarding wildlife damage to hay crops. Such surveys can provide wildlife managers with important information regarding landowner wildlife damage management needs and concerns (Conover 1994).

METHODS

We surveyed 334 alfalfa growers (4% of all alfalfa growers in Utah) whose names were on the Utah Department of Agriculture's (UDA) 1993 Hay List. The UDA maintains this list to provide information to individuals who contact the department about purchasing alfalfa hay in Utah. The UDA updates this list each January.

We included a 2-page wildlife damage survey in a UDA mailing sent to the growers. In addition to the survey, growers received a cover letter, the UDA's questionnaire, and a business reply envelope. The cover letter stated that if no response was received within 30 d, the grower's name would be removed from the hay list. A follow-up letter was sent to nonrespondents 3 wk after the initial mailing. Those failing to respond to the 2nd mailing were removed from the hay list.

The survey contained questions about the growers' experiences with wildlife in their alfalfa crops. Growers were asked to identify wildlife species causing damage to hay crops, type of damage, their annual monetary loss from wildlife damage, specific damage control techniques employed on their farm to control wildlife damage, whether they received any type of damage compensation or assistance, who they contacted for assistance and information, and what type of information and programs they found most useful in managing wildlife damage. Further, growers were asked to rate on a scale of 0 to 5 (0 = no cost through 5 = high cost) relative losses caused by different wildlife species to their alfalfa crops and the costs associated with common management practices used on their farms and ranches.

Responses were stratified and analyzed by the number of hectares in alfalfa (0–40, 41–80, 81–200, 201–400, and >400) and type of operation (irrigated or dryland). Levere's tests were used to determine equality of variances by types and sizes of alfalfa operation (SPSS 1995).

We assumed that alfalfa growers on the hay list have the same values and perceptions as the population of Utah alfalfa growers. To determine if the hay list was statistically representative of Utah alfalfa growers, we compared the mean alfalfa farm size and regional distributions of farms on the hay list with acreage categories reported by the UDA for all Utah alfalfa farms (Gneiting 1994) using a Kruskal-Wallis one-way analysis of variance. Differences in these tests were considered significant if $P < 0.05$.

RESULTS

Alfalfa Production

One hundred sixty-four completed questionnaires (49.1%) were returned, of which 150 (91%) were useable for analysis. Survey respondents reported growing 16,867 ha of alfalfa, of which 14,391 ha (85%) was irrigated and 2486 ha (15%) was dryland alfalfa. Irrigated alfalfa farms ranged in size from 5 to 1062 ha. Dryland alfalfa farms ranged in size from 3 to 320 ha. All farms were family owned and operated.

Since the UDA hay list is relatively dynamic, it contains information regarding the grower's mailing address, telephone number, and interest in selling alfalfa hay, but not the size and type of operation. Information on alfalfa operations was obtained through the survey; thus, we were unable to determine if there were any significant differences between respondents and nonrespondents.

Although the responses received constituted 2% of all Utah alfalfa growers ($N = 7600$), our sample was representative of the population based on mean farm size ($H = 7.0$; 7 df; $P = 0.001$) and regional distribution. Utah alfalfa acreage percentages reported by the UDA for northern, central, eastern, and southern regions were 30%, 31%, 19%, and 20%, respectively (Gneiting 1994). Regional alfalfa acreage percentages for our sample were northern 27%, central 34%, eastern 21%, and southern 18%.

Wildlife Species Present in Utah Alfalfa Fields

Respondents reported 20 different species of wildlife were present in their alfalfa fields. Pocket gophers and mule deer were the most abundant, being reported present on 124 (82.7%) and 120 (80.0%) farms, respectively. Other wildlife species reported by farmers as common in alfalfa fields included jackrabbits (*Lepus* spp.; $n = 89$, 59.3%), ground squirrels (*Spermophilus* spp.; $n = 83$, 55.3%), prairie dogs (*Cynomys* spp.; $n = 69$, 46.0%), waterfowl (*Anatidae*; $n = 66$, 44.0%), elk (*Cervus elaphus*; $n = 62$, 41.3%), pronghorn (*Antilocapra americana*; $n = 54$, 36.0%), and voles (*Microtus* spp.; $n = 50$, 33.3%). Wildlife species reported by farmers as being less common in alfalfa fields included marmots (*Marmota flaviventris*), badgers (*Taxidea taxus*), red foxes (*Vulpes vulpes*), sandhill cranes (*Grus canadensis*), Canada geese (*Branta canadensis*), cottontail rabbits (*Syvilagus* spp.), deer mice (*Peromyscus maniculatus*), raccoons (*Procyon lotor*), ring-necked pheasants, and muskrats (*Ondatra zibethica*).

Monetary Losses Caused by Wildlife

One hundred nine growers (72%) reported losing \$350,000 ($\bar{x}$ = \$3242, $s_{\bar{x}} = 526$) because of wildlife damage in their alfalfa fields. Monetary losses averaged \$24.79/ha.

The average dollar loss reported by respondents who grew only irrigated alfalfa was \$3016 ($n = 86$, $s_{\bar{x}} = 554$). Respondents who grew both irrigated and dryland alfalfa reported an average loss of \$4388 ($n = 21$, $s_{\bar{x}} = 1525$). Those who grew only dryland alfalfa reported an average loss of \$3750 ($n = 2$, $s_{\bar{x}} = 250$).

The highest losses per/ha were reported by respondents who grew both irrigated and dryland alfalfa (\$42 ha). Respondents who grew only irrigated or dryland alfalfa reported losses per/ha of \$19 and \$28, respectively.

Growers with irrigated alfalfa farms >200 ha in size reported significantly higher monetary losses than operations <200 ha in size ($F = 15.5$; 1,103 df; $P < 0.001$). Although the average monetary loss reported by larger alfalfa farms was \$5078 ($n = 50$) compared to \$1639 for smaller farms ($n = 55$), the average loss per/ha was higher on smaller (\$37) than larger farms (\$21; $F = 24.9$; 1,103 df; $P < 0.001$). Growers reported no significant difference in damage losses by size for irrigated/dryland alfalfa farms ($F = 0.4$; 1,26 df; $P = 0.52$).

Respondents with alfalfa farms >80 ha reported that rodents ($F = 7.9$; 1,107 df; $P = 0.006$) and ungulates ($F = 18.2$; 1,107 df; $P < 0.001$) caused higher monetary losses when compared to smaller farms (<80 ha). No significant differences in monetary losses due to waterfowl were detected by alfalfa farm size ($F = 0.006$; 1,107 df; $P = 0.940$).

Relative Costs of Wildlife Damage in Alfalfa Fields

Respondents ranked on a scale of 0–5 (0 = no cost through 5 = high cost) the relative damage costs associated with common wildlife species reported in their alfalfa fields as follows: mule deer (2.9), pocket gophers (2.4), elk (1.6), prairie dogs (1.4), ground squirrels (1.4), jackrabbits (1.3), waterfowl (1.0), pronghorn (0.7), and meadow voles (0.9). Respondents with irrigated alfalfa farms >200 ha reported that elk ($F = 7.9$; 1,56 df; $P = .007$) and pronghorn ($F = 7.5$; 1,48 df; $P = .008$) caused significantly greater cost-related problems than on smaller farms (<200 ha). Respondents with dryland alfalfa farms >200 ha reported greater significant cost-related problems caused by jackrabbits ($F = 14.1$; 1,20 df; $P = 0.001$) and mule deer ($F = 8.5$; 1,28 df; $P = 0.007$) than on smaller farms (<200 ha). Survey respondents indicated that alfalfa production problems differed by specific wildlife species (Table 1).

Farm and Ranch Management Practice Comparisons

Respondents ranked on a scale of 0–5 (0 = no cost through 5 = high cost) the relative cost of the 7 farm management practices as follows: irrigation (3.8), fertilization (3.4), weed control (2.9), insect control (2.6), fencing (2.3), big game control (2.0), and rodent/rabbit control (1.9). Fertilization, weed control, and irrigation were used on 82%, 81%, and 80% of the farms, respectively. Big game and rodent/rabbit control were used by 71% and 38% of the respondents, respectively. Respondents also reported employing several techniques to control wildlife damage in alfalfa fields (Table 2). Based on sizes and types of alfalfa operations, the only significant cost differences reported by management practices were for irrigation on farms >200 ha ($F = 5.0$; 1,124 df; $P = 0.03$).

TABLE 1. Percentage of all respondents ($N = 150$) reporting problems caused by a specific wildlife species in Utah alfalfa fields in 1993 and a breakdown of that percentage into subcategories based on the most severe type of problem caused.

		Percentage identifying a specific problem as most severe			
Wildlife species causing damage	Reporting problems (%)	Hay quality	Hay quantity	Equipment damage	Increased costs
Pocket gophers	68.7	14.0	20.7	26.0	8.0
Ground squirrel	33.3	4.0	10.7	15.3	3.3
Voles	10.7	2.7	6.7	1.3	0.0
Jackrabbits	32.8	2.7	28.7	0.7	0.7
Prairie dogs	23.3	0.7	8.0	13.3	1.3
Elk	20.0	6.0	12.7	1.3	0.0
Mule deer	64.0	8.7	54.0	1.3	0.0
Antelope	9.3	1.3	8.0	0.0	0.0
Waterfowl	17.3	2.7	14.7	0.0	0.0

Wildlife Damage Management Assistance Programs

Fourteen respondents (9%) reported receiving compensation for wildlife damage in their alfalfa fields. Of these, 12 received compensation for damage caused by mule deer. Another 48 (31%) indicated they received some type of technical assistance to control wildlife damage. Most of this assistance (75%) was provided to control damage caused by mule deer.

One hundred twenty-two respondents (80%) reported seeking either information or assistance in dealing with wildlife depredation problems. Conservation officers were cited by 53 growers (43%) as being their primary contact for information or assistance. County agents and UDWR biologists ranked 2nd (22%) and 3rd (18%), respectively. Other sources of information in order of decreasing importance were other landowners (7%), farm and ranch stores (5%), and UDA agricultural representatives (3%).

Respondents preferred compensation and incentive programs (42%) to other types of programs to manage damage caused by wildlife in alfalfa fields. Research (17%), field demonstrations (13%), workshops (13%), facts sheets (13%), and videos (14%) were rated nearly equal in usefulness.

DISCUSSION

Relationship of Perceived Damage Costs to Wildlife Management

Surveys can be cost-effective means of assessing the magnitude and economic impact of wildlife depredation (Crabb et al. 1986). Unfortunately, due to the cost and time associated with conducting reliable surveys, many wildlife agencies are unable to perform this work on a regular basis. Our experience suggests that wildlife agencies should consider using state agriculture department hay lists to conduct benchmark surveys to identify wildlife damage management concerns and needs. Most states maintain hay lists (R. Parker, personal communication, UDA, 1995).

Our results summarize perceived losses. The relationship between perceived and actual losses is unclear and probably difficult to estimate (Conover 1994). This relationship depends in part on how conspicuous the damage appears and which wildlife species causes the damage (Wakeley and Mitchell 1981, Decker et al. 1984, McIvor and Conover 1994b).

Most respondents reported problems with pocket gophers and mule deer. Other species commonly causing problems included jackrabbits, ground squirrels, prairie dogs, waterfowl, elk, pronghorn, and meadow voles. Conover (1994) also found that these species, in particular deer, were perceived to cause most damage to agricultural crops in the U.S.

Based on statewide averages, in 1993 Utah alfalfa growers harvested 10.5 tons/ha with a market value of $71.66 a ton. Survey respondents produced 177,104 tons of alfalfa on 16,867 ha having a total value of $12,691,000. The $350,000 loss reported due to wildlife represents 2.8% of the crop value. Expanding this to the total value of alfalfa produced in Utah during 1993 results in a total perceived loss of $4.4 million. This is 9 times the amount the Utah State Legislature annually appropriates ($500,000) to reimburse crop owner depredation claims and expenses (Chapter 307, Utah Code 1994b).

TABLE 2. Percentage of all respondents ($N = 150$) using a specific technique to control damage caused by wildlife species in Utah alfalfa fields in 1993 and a breakdown of that percentage into subcategories based on the most effective technique used.

		Percentage identifying a specific technique as being most effective						
Wildlife species causing damage	Using damage control techniques (%)	Trapping	Shooting/ hunting	Poison baits	Fumigants	Cultural	Fencing	Hazing
Pocket gopher	41.7	6.7	0.0	33.0	2.0	0.0	0.0	0.0
Ground squirrel	45.4	4.7	17.3	22.0	0.0	0.7	0.0	0.7
Voles	13.3	2.0	2.7	7.3	0.0	1.3	0.0	0.0
Jackrabbits	39.3	0.0	36.0	2.7	0.0	0.0	0.7	0.0
Prairie dogs	24.0	2.0	12.7	7.3	1.3	0.0	0.7	0.0
Elk	21.3	0.0	12.0	0.0	0.7	0.0	7.3	1.3
Mule deer	46.7	0.0	22.7	0.0	0.7	0.0	16.0	7.3
Antelope	9.7	0.0	4.0	0.0	0.7	0.0	2.7	1.3
Waterfowl	16.7	0.0	13.3	0.7	0.7	0.0	0.0	2.0

Utah Code authorizes the UDWR to immediately pay any approved damage claims ≤ \$500. Claims or total amounts of claims submitted by a claimant in the fiscal year that are >\$500 are not paid until the total amount of approved claims for the fiscal year is determined. If the amount claimed exceeds the appropriation, the per claimant amounts paid in excess of \$500 are prorated. The current appropriation falls short of satisfying wildlife damage compensation claims and expenses (R. Valentine, personal communication, UDWR, 1996).

If 13% of Utah alfalfa growers ($n = 1000$) submitted approved claims of \$500, their claims would deplete the annual appropriation. Although the alfalfa growers we surveyed preferred compensation and incentive payments over other types of wildlife damage management programs, only 9% had ever received any financial support.

In the United States, 2.1 million farmers control 400 million ha of our 937 million ha land base. Their actions largely influence the quality and quantity of the existing wildlife habitat base (Gerard 1995). Landowners' perceptions and concerns about wildlife damage are important because they influence their attitudes and behavior toward wildlife. Conover (1994) suggested that wildlife damage has reached levels that discourage private landowners from managing for wildlife on their property. Our results suggest that Utah alfalfa growers also perceive wildlife damage in alfalfa fields as a serious concern. Although wildlife professionals working for federal or state wildlife and agricultural agencies believe that wildlife damage has increased in the last 30 yr, our survey results reinforce Conover and Decker's (1991) suggestion that programs necessary to adequately address crop owner concerns have not yet been implemented.

Role of State Agencies in Resolving Wildlife Damage Management Concerns

State wildlife management agencies are responsible for managing damage caused by big game, upland game, and waterfowl (Musgrave and Stein 1993). State agriculture departments administer and enforce pesticide control legislation that regulates the safe and proper use of pesticides for vertebrate pest damage. Because of this role, agriculture departments have jurisdiction over the control of unprotected wildlife species (vertebrate pests). In Utah these include pocket gophers, field mice, muskrats, ground squirrels, jackrabbits, raccoons, skunks, red fox, and coyotes.

The UDWR recognizes that private lands within Utah provide habitat for wildlife and that under some circumstances wildlife may cause economic losses to the landowner. With this understanding, the UDWR cooperates with the UDA and the U.S. Department of Agriculture Animal Plant Health and Inspection Service/Animal Damage Control (ADC) program to conduct predator, bird, and rodent control activities and compensate landowners for certain losses caused by wildlife using funds appropriated by the legislature.

In 1994 the Utah legislature enacted an alternative compensation program that allows landowners to receive permits to harvest antlerless animals as mitigation for damage caused by big game (Chapter 176, Utah Code 1994a). In 1995 the UDWR Southern Region issued >1200 mitigation permits, of which 50% were filled. In 1996 both the number of tags issued and number of animals harvested declined as landowners lost interest in the program (N. McKee, personal communication, UDWR, 1996).

To better address landowners' concerns given fiscal and legal constraints, we suggest that agencies and organizations responsible for managing wildlife resources and wildlife damage on Utah agricultural lands collaborate to develop strategies that allow profitable agriculture and wildlife to coexist. Utah's posted hunting unit (PHU; Chapter 288, Utah Code 1993b) and wildlife habitat authorization (WHA) programs (Chapter 75, Utah Code 1995) may offer additional mechanisms to achieve this goal.

The Posted Hunting Unit Program

The UDWR also recognizes that wildlife can be a significant benefit to the landowner. The PHU program provides landowners with monetary incentives, through an allocation of hunting permits, to include wildlife (small game, waterfowl, and big game) in farm and ranch management plans. Landowners who participate in the program are required to improve wildlife habitat but are ineligible to receive compensation for crop losses caused by wildlife.

The most successful of Utah's PHU programs involves big game animals. In 1994, 47 big game PHU programs, encompassing over 400,000 ha of private land, provided additional economic returns for hundreds of landowners and hunting experiences for thousands of hunters. Current program guidelines limit participation to landowners or landowner groups who own at least 4000 ha (Chapter 288, Utah Code 1993b). The size limitation was established to create more manageable herd units.

In our survey, respondents reported that big game animals caused the greatest damage. We suggest that big game PHU guidelines be modified to accommodate farm or ranch units <4000 ha in size. This modification would provide the stimulus necessary to alleviate many crop owners' wildlife damage concerns and provide an additional incentive to include wildlife in farm and ranch management plans. In addition, we suggest that big game PHU operators be encouraged to incorporate provisions in their wildlife management plans to compensate smaller nonparticipating landowners adjacent to their operation for crop damage caused by big game animals.

The Wildlife Habitat Authorization Program

The WHA program requires persons 14 yr of age or older to purchase a wildlife habitat authorization prior to purchasing certain hunting or fishing licenses or permits. The funds generated from this authorization are placed into a restricted account to be used for wildlife habitat improvements. Several other Great Basin states operate similar programs designed to generate funds to do habitat work.

We recommend that state wildlife agencies consider using habitat funds to implement and evaluate enhancement projects and programs on public and private land that are designed specifically to reduce big game depredation on private land. Habitat funds could be used to establish big game lure crops, situate interceptor strips, or modify migration corridors as a means of abating localized depredation problems.

Wildlife Damage Education Needs

Crop owners also need additional information on techniques used to manage wildlife damage. Several respondents reported using fumigants and poison baits to control damage caused by ungulates, lagomorphs, and birds. These practices are illegal, as no products are currently registered in the U.S. to control damage caused by these species.

We recommend that state wildlife agencies, agriculture departments, and federal ADC programs cooperate in the development of public outreach, extension education, and research activities intended to inform crop owners about techniques that can be used to manage wildlife damage. These programs also should provide information on conservation technologies, nonlethal strategies, and opportunities that can be used to control wildlife damage and benefit wildlife resources while maintaining or enhancing agricultural profitability.

In conclusion, previous studies conducted in the Great Basin focused on evaluating the effects of big game depredation (Tebaldi and Anderson 1982, Austin and Urness 1987a, 1987b, 1989, 1993) and sandhill cranes (McIvor and Conover 1994b) on agricultural production. Our study adds to this research by providing important insights regarding crop owners' perceptions about wildlife damage and their needs and preferences in managing damage.

Our results suggest that Utah alfalfa growers perceive wildlife damage as a serious concern. This concern should be shared by wildlife managers.

In addition to informing landowners of their concern over wildlife damage, wildlife managers should demonstrate it by addressing potentials for increasing damage on private lands when developing wildlife habitat management plans (Conover 1994). Wildlife managers also should incorporate strategies in management plans to benefit wildlife and reduce depredation potentials on private land.

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SPATIAL RELATIONSHIPS AMONG YOUNG *CERCOCARPUS LEDIFOLIUS* (CURLLEAF MOUNTAIN MAHOGANY)

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ABSTRACT.—This study analyzed spatial location patterns of *Cercocarpus ledifolius* Nutt. (curlleaf mountain mahogany) plants, classified as current-year seedling, established seedling, juvenile, and immature individuals, at a central Nevada study site. Most current-year seedlings were located in mahogany stands in which large, mature individuals had the greatest abundance. These stands had greater litter cover and a thicker layer of litter than areas with few current-year seedlings. Most established young *Cercocarpus* were located in adjacent *Artemisia tridentata* ssp. *vaseyana* (mountain big sagebrush) communities, or in infrequent canopy gaps between relatively few large, mature *Cercocarpus*. We discuss potential roles of plant litter, root growth characteristics, nurse plants, and herbivory in the establishment and renewal of *Cercocarpus* communities.

Key words: Cercocarpus, *litter, mountain mahogany, seedling, recruitment, spatial relationships, maturity class.*

Cercocarpus ledifolius Nutt. (curlleaf mountain mahogany; hereafter *Cercocarpus*) is a desirable browse species in the Intermountain West (Smith 1950, Smith and Hubbard 1954, Hoskins and Dalke 1955). Attempts to revegetate wildlife habitat with *Cercocarpus* have had little success. Common problems have been competition from annual weeds (Holmgren 1954), sensitivity to frost and drought (Plummer et al. 1957, 1968), slow growth (Plummer et al. 1957), and impaired germination (Liacos and Nord 1961, Young et al. 1978).

Cercocarpus does not sprout from root crowns following removal of the canopy (Ormiston 1978, Austin and Urness 1980). Reproduction must occur from seed. Limited research has addressed the structure of *Cercocarpus* stands (Scheldt 1969, Duncan 1975, Davis 1976, Davis and Brotherson 1991) or how stand structure may influence regeneration. Except for Duncan's (1975) work in Montana, past studies concluded that most stands have few young *Cercocarpus* and that older individuals have the greatest abundance. These studies (Scheldt 1969, Duncan 1975, Davis 1976, Davis and Brotherson 1991) also found few seedlings, low seedling survival, and irregular seed production (Plummer et al. 1968). The few current-year *Cercocarpus* seedlings that emerge apparently have rapid elongation of their taproot (0.97 m after 120 days; Dealy 1975). Rapid root growth should benefit *Cercocarpus* seedlings in the Great Basin, where a semiarid climate predominates. Previous studies indicate land managers require additional information about 2 processes in *Cercocarpus* communities: (1) the dynamics of current-year *Cercocarpus* seedlings in relationship to the rest of the vegetative community, and (2) conditions that permit current-year seedlings and established young *Cercocarpus* to be recruited into the population structure.

Schultz et al. (1991) presented the first predictive relationships about the structure of *Cercocarpus* stands. Their study in western and central Nevada found that mean *Cercocarpus* crown volume had a significant ($P \leq 0.05$) inverse relationship ($r^2 = 0.78$) with density of *Cercocarpus* in established seedling, juvenile, and immature maturity classes. Schultz (1987) also found that *Cercocarpus* canopy cover and mean *Cercocarpus* crown volume had significant ($P \leq 0.05$) positive correlations with density of current-year *Cercocarpus* seedlings. This dichotomy, along with other patterns observed by Schultz (1987), may offer valuable insight into the regeneration of *Cercocarpus* stands. Additionally, Schultz (1987) observed that (1) locations with large canopy gaps between widely scattered mature individuals generally had more *Cercocarpus* in established seedling, juvenile, and immature maturity classes than did locations with small canopy gaps; (2) locations with small canopy gaps, and hence greater *Cercocarpus* canopy cover and crown volume, had a greater abundance of young *Cercocarpus* in adjacent *Artemisia tridentata* ssp. *vaseyana* (mountain big sagebrush) communities; (3) established *Cercocarpus* in the *Artemisia* community were often rooted under the protective canopy of another shrub or shrub skeleton; and (4) most current-year *Cercocarpus* seedlings were found where thick plant litter had accumulated under mature *Cercocarpus*. Table 1 summarizes differences (patterns) in *Cercocarpus* stand structure from locations in western (Peavine Mountain) and central (Shoshone Range) Nevada. Table 2 defines the maturity classes mentioned throughout this study.

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Based on observations about the spatial location of current-year *Cercocarpus* seedlings and established *Cercocarpus* in the youngest maturity classes, we implemented a brief descriptive study on the Shoshone Range in central Nevada to quantify the spatial distribution of current-year *Cercocarpus* seedlings and *Cercocarpus* in established seedling, juvenile, and immature maturity classes. We integrate data from this study, the Schultz et al. (1990, 1991) studies about stand structure, which were conducted at the same location as this study, and other relevant literature to describe possible processes, mechanisms, or factors that influence survival of current-year *Cercocarpus* seedlings and their subsequent recruitment into established seedling, juvenile, and immature maturity classes. Our goal is to stimulate thought that can guide research about the regeneration of this desired browse species.

METHODS

Initial measurements describing the structure of *Cercocarpus* stands occurred on the Shoshone Range and Peavine Mountain in June and July 1985. Relevant results are presented in Table 1. Measurements describing the spatial location of individuals in current-year *Cercocarpus* seedling, established seedling, juvenile, and immature maturity classes were made on the Shoshone Range in early August 1985. Abundant rainfall in central Nevada during June and July allowed current-year *Cercocarpus* seedlings to survive until we initiated this study. Similar data could not be collected from Peavine Mountain in western Nevada because a dry spring and summer resulted in the early desiccation and disappearance of most *Cercocarpus* seedlings.

Seven 1 × 40-m belt transects (BT) were located at 4 of the 13 *Cercocarpus* stands in the Shoshone Range measured by Schultz et al. (1990, 1991). None of the BTs were placed in study plots sampled by Schultz et al. (1990, 1991; also described in Schultz 1987) because those study plots were located in the interior of the stands, not near the ecotone with the adjacent *Artemisia* community. The 4 stands sampled were selected because (1) they were near access roads and time was limited, and (2) their respective topographic positions allowed at least 1 transect (of the 7) to be located at each cardinal aspect.

The following criteria were used to select transect locations: (1) a *Cercocarpus* stand dominated by mature individuals was present, (2) a sharp ecotone existed between the *Cercocarpus* stand and adjacent *Artemisia* community, (3) the transect remained on the same landform

Table 1. Mean values for structural characteristics of *Cercocarpus* communities from 2 mountain ranges in western and central Nevada (data from Schultz 1987, Schultz et al. 1990). Mean values in the same column followed by the same letter are not significantly different ($P \leq 0.05$).

Mountain range	Current-year seedlings (#/m^{-2})	Established seedling, immature, and juvenile (#/ha)	Mature *Cercocarpus* (#/ha)	*Cercocarpus* crown volume (m^3/plant^{-1})	*Cercocarpus* cover (%)	Litter cover (%)	Bare ground[1] (%)
Peavine	0.1a	922a	233a	5.8a	56a	67a	10a
Shoshone	1.9b	111b	344b	39.5b	79b	76b	10a

[1] includes gravel

Table 2. *Cercocarpus* maturity classes. Descriptions were developed from a reconnaissance of *Cercocarpus* stands near Reno, NV.

Current-year seedling	Germinated during the current growing season; usually has 4 leaves.
Established seedling	Plants ≥ 1 year of age; 2–7 mm basal diameter; smooth bark; may be up to 30 cm tall; 8 or more leaves.
Juvenile	Young plants >7 mm basal diameter; smooth bark; plants to 60 cm tall.
Immature	Young plants >1.25 cm basal diameter; smooth bark; plants to 1.5 m tall.
Young-mature	Cracked bark; 1.5–3.0 m tall; crown broadened; may be multistemmed from base; not suppressed by adjacent larger mountain mahogany plants.
Mature	Cracked bark; wide full crown; few dead branches; may have several stems from base; >3 m tall.
Over-mature	Cracked bark; may be multistemmed; numerous dead branches; may be >3 m tall; frequently suppressed by adjacent larger mountain mahogany plants.

Table 3. Elevation, slope, and aspect of each belt transect in which count data were obtained.

Transect	Elevation (m)	Slope (%)	Aspect (degrees)
1	2688	41	80
2	2688	41	80
3	2688	41	80
4	2400	29	290
5	2758	34	0
6	2758	34	0
7	2758	25	168

and had the same aspect throughout its length, and (4) all transects located in the same stand were 40 m or more apart. Table 3 describes the elevation, slope, and aspect of each transect. *Cercocarpus* in the Shoshone Range are largely restricted to the Foxmount soil series (Carol Jett personal communication), which is a gravelly loam (specifically, a Loamy-skeletal, mixed Topic Cryboroll). This soil is well drained and moderately permeable. Depth to a paralithic contact averages 60–100 cm.

All transects were located such that 20 m occurred in the *Cercocarpus* stand and 20 m in the adjacent *Artemisia* community. Each transect was divided into forty 1 × 1-m quadrats. Every *Cercocarpus* rooted in each quadrat was classified by maturity class. For *Cercocarpus* in established seedling, juvenile, and immature maturity classes, we determined whether the plant was rooted under the protective canopy of a live or dead shrub.

Distribution of current-year seedling, established seedling, juvenile, and immature *Cercocarpus* was summarized for 10 classification categories (populations). These were (1) the number of *Cercocarpus* in current-year seedling, established seedling, juvenile, and immature maturity classes rooted in either the *Cercocarpus* community or the adjacent *Artemisia* community, and (2) the number of established seedling, juvenile, and immature *Cercocarpus* rooted under and not under the canopy of a live or dead shrub. The Wilcoxon signed rank test was used to determine if there was a significant difference in the distribution of individuals in the *Cercocarpus* and *Artemisia* communities, respectively, for each maturity class. The significance level is $P \leq 0.05$ unless otherwise noted.

Results

Current-year *Cercocarpus* seedlings were not distributed evenly between *Cercocarpus* stands and adjacent *Artemisia* communities (Table 4). Significantly more current-year seedlings were rooted in the *Cercocarpus* community.

At least 81% of established seedling, juvenile, and immature *Cercocarpus* were rooted in the adjacent *Artemisia* community (Table 4). For established seedling and juvenile maturity classes the difference in spatial distribution was significant; the significance level for immature *Cercocarpus* was $P \leq 0.06$.

More established seedling, juvenile, and immature *Cercocarpus* were rooted under the protective canopy of a live or dead shrub than in the open (Table 5). Only 1 transect had more plants without a protective canopy, but the significance level was $P \leq 0.10$.

Discussion

Spatial distribution of current-year *Cercocarpus* seedlings and established young *Cercocarpus* had an inverse relationship (Tables 1, 4). Current-year seedlings were most abundant in *Cercocarpus* stands dominated by large, mature *Cercocarpus* and least abundant in adjacent *Artemisia* communities. Young, established

TABLE 4. Number of current-year seedling, established seedling, juvenile, and immature mahogany rooted in *Cercocarpus* (CER) stands dominated by mature individuals, and in adjacent *Artemisia* (ART) communities. Within each maturity class, total values between community types with different letters are significantly different ($P \leq 0.05$).

	Current-year seedling		Established seedling		Juvenile		Immature	
Transect	CER	ART	CER	ART	CER	ART	CER	ART
1	20	0	1	11	1	5	0	1
2	72	15	1	15	3	3	0	5
3	75	53	0	16	0	6	5	6
4	31	39	0	2	0	7	0	4
5	337	25	0	11	0	19	0	0
6	506	28	1	11	0	4	0	0
7	33	0	1	9	0	2	0	5
Total	1074a	160b	4a	75b	4a	46b	5a	21a[1]
Percent	87	13	5	95	8	92	19	81

[1] Significantly different at $P \leq 0.06$.

Cercocarpus were virtually absent from mature *Cercocarpus* stands but had a greater abundance in adjacent *Artemisia* communities (Tables 1, 4). Young *Cercocarpus* were also abundant in stands with low *Cercocarpus* crown cover or relatively few large *Cercocarpus* (Table 1). The low density of current-year seedlings in adjacent *Artemisia* communities (Table 4) has 2 possible interpretations: (1) viable *Cercocarpus* seeds were not dispersed into the *Artemisia* community, or (2) germination of *Cercocarpus* seed was impaired. Because data about seed densities are lacking, a definitive conclusion cannot be made. *Cercocarpus* seed, however, is primarily wind dispersed (USDA 1948); therefore, it is unlikely that few seeds were present in the *Artemisia* community, particularly since all data were collected within 20 m of the *Cercocarpus* stands. Most likely, over 85% fewer *Cercocarpus* seedlings were in the *Artemisia* community (Table 4) because seed germination was substantially lower than in the *Cercocarpus* stands.

The inverse relationship for distribution of current-year seedlings and established young *Cercocarpus* indicates that locations with a high abundance of current-year seedlings are not necessarily locations with the best seedling survival. Populations perpetuate when seedlings survive and advance into successively older maturity classes, eventually producing new seedlings. The pattern for spatial distribution of current-year seedling, established seedling, juvenile, and immature *Cercocarpus* derived from this study and that conducted by Schultz et al. (1990, 1991) indicates that 4 factors may influence survival of current-year seedlings as well as plants in the youngest maturity classes: (1) presence or thickness of plant litter, (2) root growth characteristics, (3) presence of nurse plants, and (4) herbivory.

Moderate levels of litter can favor seed germination and seedling establishment by decreasing soil temperature and increasing soil moisture (Evans and Young 1970). Thick litter, however, can reduce seedling establishment and survival by preventing or restricting contact between soil and seed or soil and root (Fowler 1986).

High litter cover (Table 1) and a thick layer of litter (personal observation) were common in *Cercocarpus* stands in the Shoshone Range. Litter cover and litter thickness were not measured in adjacent *Artemisia* communities; however, litter cover in high-elevation (>2200 m) *Artemisia* communities ranges from 15% to 50% (Tueller and Eckert 1987). Extensive and deep litter in *Cercocarpus* stands may promote seed germination but decrease seedling survival because roots from *Cercocarpus* seedlings seldom make contact with the mineral soil. Less litter in the *Artemisia* community may reduce *Cercocarpus* seed germination but enhance survival of seeds that germinate. Root growth characteristics may play an important role.

Rapid root growth that current-year *Cercocarpus* seedlings experience (Dealy 1975) should enhance survivorship of *Cercocarpus* seedlings during seasonal drought, a common phenomenon in the Great Basin. Root systems that undergo rapid elongation should be able to follow a retreating zone of soil moisture (downward) better than root systems that elongate slowly. We excavated several *Cercocarpus* seedlings rooted in thick plant litter and found that root growth was extensive (20+ cm) but not

TABLE 5. The number of established seedling, juvenile, and immature *Cercocarpus* rooted under and not under another shrub or shrub skeleton. Significance level is $P \leq 0.10$.

Transect	Rooted under	Not rooted under
1	16	3
2	23	4
3	20	13
4	8	5
5	6	24
6	9	7
7	15	2
Total	97a	58b
Percentage	63	37

downward toward or into the mineral soil. Root growth was largely lateral. Following germination in early spring, available moisture in both mineral soil and plant litter is probably high, since cool temperatures and abundant precipitation are common (Houghton et al. 1975). Because moisture is not limiting early in the growing season, root growth probably follows the path of least resistance. When thick litter resides on top of mineral soil, the path of least resistance would be laterally through the litter, not downward through the mineral soil. The loamy soil that *Cercocarpus* stands inhabit undoubtedly stores and retains more water than plant litter does, and thus should desiccate more slowly. If thick plant litter prevents or retards roots of current-year *Cercocarpus* seedlings from reaching or penetrating moist mineral soil, seedling mortality should be high when litter desiccates rapidly later in the summer. We observed high mortality for current-year *Cercocarpus* seedlings in August in *Cercocarpus* stands with thick accumulations of litter. Less litter on Peavine Mountain (Table 1) and in the *Artemisia* community (see Tueller and Eckert 1987) may enable root systems of *Cercocarpus* seedlings at these locations to grow downward into mineral soil immediately following germination. This should increase survivorship of current-year seedlings, which may account (at least partially) for the greater abundance of established seedling, juvenile, and immature *Cercocarpus* on sites with less surface litter.

Herbivory may also play a role in seedling survival. Current-year *Cercocarpus* seedlings have an average leaf surface area of only 4 cm^2 (Dealy 1975), which herbivores can easily consume. Herbivory can adversely affect establishment of woody species (Marquis 1974, McAuliffe 1986), including *Cercocarpus* (Scheldt and Tisdale 1970). The presence of protective nurse plants, therefore, may be important for regeneration of *Cercocarpus* seedlings.

Cercocarpus stands in the Shoshone Range had a mean shrub canopy cover of 11% (Schultz et al. 1990). Total shrub canopy cover was not measured in adjacent *Artemisia* communities; however, it generally ranges from 41% to 50% (Tueller and Eckert 1987). Thus, shrub cover in adjacent *Artemisia* communities is 3.5 to 4 times greater than that in *Cercocarpus* stands. Since more established seedling, juvenile, and immature *Cercocarpus* were rooted under a shrub or shrub skeleton than not (Table 5), the difference in shrub canopy cover between *Cercocarpus* stands and adjacent *Artemisia* communities may influence survival of current-year seedlings, established seedlings, juvenile, and immature *Cercocarpus*. *Artemisia* and other short-statured shrubs may serve as nurse plants and protect small *Cercocarpus* (including current-year seedlings) from herbivores until their photosynthetic surface is large enough to cope with frequent browsing. Since shrub cover is low in *Cercocarpus* stands, more young *Cercocarpus* are probably exposed to herbivores than in *Artemisia* communities. This may help explain the near absence of young *Cercocarpus* in *Cercocarpus* stands and their greater abundance in adjacent *Artemisia* communities.

CONCLUSIONS

Abundance of current-year *Cercocarpus* seedlings is greatest in *Cercocarpus* stands that have high *Cercocarpus* canopy cover, large mean *Cercocarpus* crown volume, and an extensive layer of plant litter. These stand attributes also result in a low density of plants in established seedling, juvenile, and immature maturity classes. Established young *Cercocarpus* are most abundant where gaps occur in the *Cercocarpus* canopy, or in adjacent *Artemisia* communities. Survival of current-year seedlings appears best at locations that permit roots of seedlings to make contact with mineral soil. Survival of current-year seedlings and progression of individuals from established seedling maturity class into successively older maturity classes appear to be enhanced by the presence of a shrub canopy that protects small *Cercocarpus* from herbivores.

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POTENTIAL FOR CONTROLLING THE SPREAD OF *CENTAUREA MACULOSA* WITH GRASS COMPETITION

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ABSTRACT.—Spotted knapweed (*Centaurea maculosa* Lam.) is a major rangeland and roadside weed of the northern Rocky Mountains. It is often found in plant communities dominated by *Pseudoroegneria spicatum* or *Festuca idahoensis*, but it rarely invades roadsides dominated by *Bromus inermis* Leyss. Aboveground biomass of the 3 grass species grown in mixture with *Centaurea* was compared to growth in monoculture at a range of nitrogen input levels. The results suggest that *Bromus* is capable of suppressing the growth of *Centaurea* with the degree of suppression increasing with increasing nitrogen levels. The 2 native grasses had no impact on *Centaurea* under the controlled environment conditions of this study.

Key words: competition, weed control, Centaurea maculosa, Bromus inermis, Agropyron spicatum, Festuca idahoensis, *exotic plants.*

Centaurea maculosa Lam. (spotted knapweed) is a major weed associated with spring wet–summer dry areas of the northern Rocky Mountains (Forcella and Harvey 1981, Tyser and Key 1988, Weaver et al. 1989). *Centaurea* dominates waste places, invades disturbed rangeland, and sometimes invades undisturbed range (Tyser and Key 1988). In contrast, it rarely invades roadsides dominated by *Bromus inermis* Leyss. (Weaver et al. 1989). This suggests that it may be excluded from waste places that are planted to *Bromus* before *Centaurea* invades. Alternatively, because planting exotics violates the charge of national park managers, one may ask whether *Centaurea* might also be excluded from disturbed areas by planting native grasses that naturally dominate either relatively dry (*Pseudoroegneria spicatum* [Pursh] Scribner and Smith = *Agropyron spicatum*) or more moist (*Festuca idahoensis* Elmer.) foothill habitats.

Weed suppression may be accomplished by (1) preempting resources with more competitive plant species or (2) using biocontrols or herbicides that selectively increase weed mortality, decrease vigor, or prevent reproduction (Lindquist et al. 1995). This study considers management of *Centaurea maculosa* by competition rather than by common herbicide and biocontrol methods. This approach deserves attention because it may be less expensive and more effective than herbicides in the long term.

Our objective was to measure the competitive ability of 3 grass species against *Centaurea* in 2-way interaction experiments in sand culture. Mixture and monoculture treatments were tested for 12 wk at 5 positions on a nitrogen gradient to determine whether competitive relations were influenced by differences in nitrogen availability. A plant's ability to compete is related to its growth rate or ability to gain biomass relative to associated species (Harper 1977). We compared aboveground biomass of each species grown in mixture with *Centaurea* to its growth in monoculture.

MATERIALS AND METHODS

The rhizomatous exotic pasture grass *Bromus inermis* Leyss. and 2 native bunchgrasses normally dominating relatively dry foothills (*Pseudoroegneria spicatum*) or moister grasslands immediately above and below the conifer zone (*Festuca idahoensis*) were grown in 2-species mixtures (replacement series) with *C. maculosa*.

Experiments consisted of 3 competition treatments (monocultures of both grass and *Centaurea*, and 50:50 mixture) combined with 5 nitrogen addition treatments. Each treatment combination had 10 replicates. Within each experiment, pots were arranged in a completely randomized design on a greenhouse bench and rotated weekly to minimize position effects. Each experiment was subject to different light

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conditions because of its position in the greenhouse. A square planting pattern was used with 4 plants spaced 5 cm apart. In each pot in the mixture treatments, plants of the same species were located on the diagonal.

Seeds were planted at a depth of 1.0 cm in 1000-cm^3 pots filled with coarse washed sand. Pots were watered daily for 1 wk to allow seedling establishment. Excess seedlings were thinned and remaining seedlings allowed to grow for an additional week prior to the addition of nutrients. The basic nutrient solution was balanced with respect to all essential nutrients but could be varied to allow the establishment of nitrogen levels from 0%, 1%, 10%, 30%, and 100% of a standard level (Machlis and Torrey 1956). Sufficient nutrient solution (200 ml) was applied to saturate the pot twice weekly and water (200 ml) was added once each week. Regular watering with nutrient solution and alternate washing with tap water held the soil solution near the applied level and prevented any concentration of the soil solution due to evapotranspiration. Experiments were conducted during March, April, and May 1988, when greenhouse temperatures ranged from 14° to 32° C (25° C mean).

Twelve weeks after emergence, plants in each pot were clipped at the soil surface, separated by species, dried at 45° C for 5 d, and weighed.

Nonlinear regression procedures (SAS 1988, Gauss-Newton least squares estimation method) were used to fit a rectangular hyperbola equation [1] (Cousens 1985) to mixture and monoculture data for each species:

$$B = \frac{I_i \cdot N}{(1 + \frac{I_i \cdot N}{A_i})} \qquad [1]$$

where B = aboveground dry biomass (g $plant^{-1}$), A_i = maximum aboveground biomass of species i (g $plant^{-1}$), N = relative nitrogen addition level, and I_i = biomass of species i as relative nitrogen addition level approaches zero.

To determine the relative success of *Centaurea* in competition with each grass species, estimates of A_i and I_i were compared between mixtures and monocultures using the extra sum of squares procedure (Ratkowsky 1983, Lindquist et al. 1996). In addition, relative competition intensity (RCI; Grace 1995) was calculated to determine whether competitive relationships varied across relative nitrogen levels. RCI is calculated as

$$RCI = (B_{mono} - B_{mix})/B_{mono} \qquad [2]$$

where B_{mono} and B_{mix} are the aboveground dry biomass (g $plant^{-1}$) for a species grown in monoculture and mixture, respectively. A negative RCI value indicates that the species performs better in mixture than in monoculture. RCI may be the best measure for determining species displacement under competitive conditions across a resource gradient (Grace 1995). Analysis of variance was used to test for differences in RCI within a species across nitrogen treatments. Student's t was used to compare RCI between species at each nitrogen addition level.

RESULTS

A hyperbolic relationship between individual plant biomass and relative nitrogen level was found in all mixtures and monocultures (Figs. 1a–f). Estimates of I_i (biomass at intercept) differed between mixtures and monocultures only for *Centaurea* grown in mixture with *Bromus* (Table 1). Estimates of A_i (maximum biomass) differed for *Bromus* and *Centaurea* (Table 1).

Relative competition intensity was significantly negative for *Bromus* at all nitrogen addition levels; it varied from negative values at low nitrogen to positive values at higher nitrogen levels for *Centaurea* in competition with *Bromus* (Fig. 2). However, RCI did not differ from zero in the experiments where *P. spicatum* and *F. idahoensis* were in competition with *Centaurea* (data not shown).

DISCUSSION

Growth response of *Bromus* to nitrogen was greater in mixture with *Centaurea* than in monoculture, as indicated by the regression lines (Fig. 1a) and the negative RCI values across all nitrogen addition levels (Fig. 2). In contrast, growth response of *Centaurea* was lower in mixture with *Bromus* than in monoculture (Fig. 1). The increase in *Centaurea* RCI at high relative nitrogen level indicates that *Bromus* is a better competitor in the high nitrogen treatments (Fig. 2). Results suggest that *Bromus* is capable of suppressing the

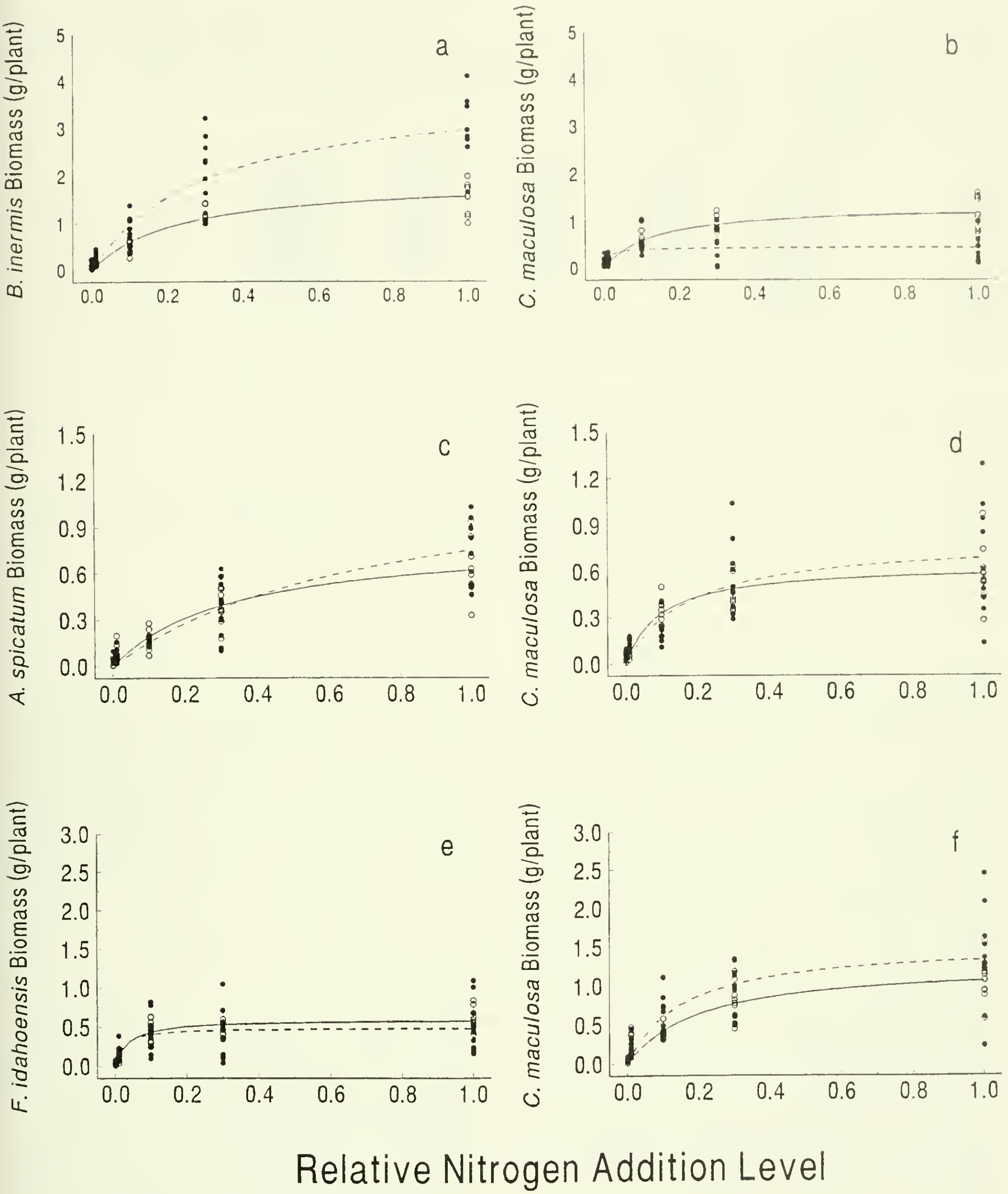

Fig. 1. Plot of observed (○) and predicted (●) aboveground dry biomass plant^{-1} on relative nitrogen addition level when grown in monoculture (____) and mixture (----): a, *Bromus* grown in monoculture and in mixture with *Centaurea*; b, *Centaurea* grown in monoculture and in mixture with *Bromus*; c, *Pseudoroegneria* grown in monoculture and in mixture with *Centaurea*; d, *Centaurea* grown in monoculture and in mixture with *Pseudoroegneria*; e, *Centaurea* grown in monoculture and in mixture with *Festuca*; f, *Festuca* grown in monoculture and in mixture with *Centaurea*.

TABLE 1. Estimates of parameter values followed by asymptotic standard errors for maximum aboveground biomass (g plant^{-1}) (A), biomass as relative nitrogen level approaches zero (I), and the coefficient of determination (r^2) obtained from fitting equation [1] to monoculture and mixture data of each species. Variation in I and A between competition treatments was tested using the extra sum of squares principle, with P value indicating the significance level for the comparison of parameter (Coeff) values from the monoculture and mixture regressions.

Species	Coeff	Competition treatment		*P* value
		Monoculture	Mixture	
Bromus	A	1.884(0.115)	3.819(0.361)	<0.000
	I	8.769(1.141)	12.893(2.197)	0.283
	r^2	0.90	0.84	
Centaurea with *Bromus*	A	1.306(0.082)	0.438(0.056)	<0.000
	I	10.621(1.861)	45.717(35.47)	0.023
	r^2	0.85	0.14	
Pseudoroegneria	A	1.289(0.237)	0.827(0.087)	0.081
	I	1.758(0.323)	2.490(0.442)	0.410
	r^2	0.80	0.82	
Centaurea with *Pseudoroegneria*	A	0.636(0.048)	0.805(0.107)	0.307
	I	6.770(1.639)	4.617(1.454)	0.665
	r^2	0.77	0.60	
Festuca	A	0.595(0.029)	0.491(0.056)	0.303
	I	16.747(3.892)	23.921(14.925)	0.857
	r^2	0.83	0.39	
Centaurea with *Festuca*	A	1.262(0.114)	1.522(0.172)	0.514
	I	6.418(1.295)	10.061(2.870)	0.535
	r^2	0.77	0.66	

growth of *Centaurea*, the degree of suppression increasing with increasing nitrogen levels.

Growth response of *Pseudoroegneria* and *Festuca* to nitrogen when growing in mixture with *Centaurea* did not differ from their response in monoculture. Likewise, growth response of *Centaurea* did not differ between monoculture and mixtures with *Pseudoroegneria* or *Festuca*. Therefore, these results suggest that these native grasses are not likely to increase or suppress growth of *Centaurea*, regardless of nitrogen addition level. This result is contrary to the observed invasion of *Centaurea* into communities dominated by these grasses. One explanation may be that disturbance (especially grazing) in the field creates gaps in the grass community where *Centaurea* can establish itself even though it is not a superior competitor for resources.

Competitive interactions were greater between each grass species and *Centaurea* at the high end of the nitrogen gradient. This may be a function of rapid growth. Thus, in nitrogen-rich environments fast-growing plants may rapidly occupy space and usurp resources to the exclusion of slow-growing species (Grime 1979, Radosevich and Holt 1984). Similar competitive effects may be expected to occur on other soil resource gradients, assuming adaptations for acquisition of nitrogen and other mobile nutrients, as well as water, are similar (Grime 1979, Fitter and Hay 1987). In addition, one may hypothesize, based on the resource ratio theory (Tilman 1982), that *Bromus* is a superior competitor for nutrients other than nitrogen relative to *Centaurea*. By increasing nitrogen, both species should be limited by essential nutrients other than nitrogen, and the species with the lowest R* (the superior competitior) for the other nutrients should displace the species with the higher R* for the same nutrients (Tilman 1990).

The ability of *Bromus* to out-compete *Centaurea* in nutrient culture provides one explanation for the observed population dynamics of *Centaurea* in the field. Roadsides seeded with *Bromus* are rarely invaded by *Centaurea* (Weaver et al. 1989). Both field and laboratory observations suggest that disturbed sites seeded simultaneously with *Centaurea* and the exotic, *Bromus*, will be dominated by *Bromus*. The effectiveness of *Bromus* in suppressing *Centaurea* may be increased with fertilization. Furthermore, it may be expected that established *Bromus* plants will suppress the growth of *Centaurea* seedlings. The results of this study suggest that at the seedling stage *Bromus* may be used to competitively exclude *Centaurea*. This method of weed management merits trial in the field. On the other hand, the regional dominants,

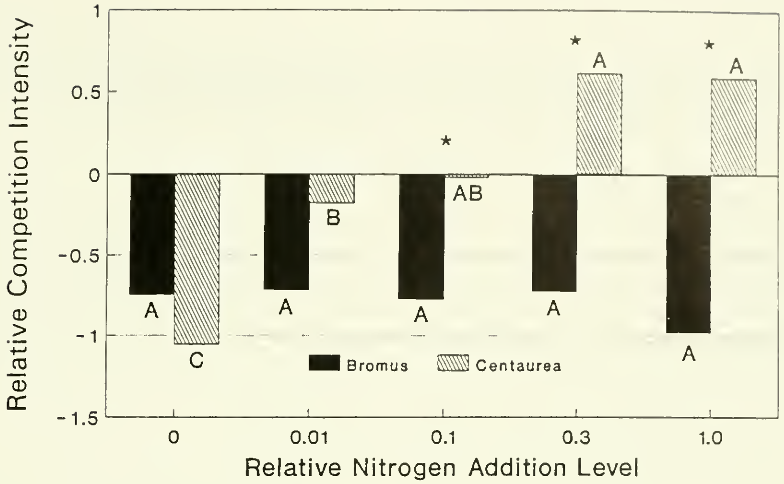

Fig. 2. Relative competition intensity (RCI) of *Bromus* and *Centaurea* across 5 relative nitrogen addition levels. Letters above bars indicate whether RCI varies (Duncan's multiple range test, $P < 0.05$) within species across nitrogen level. An asterisk indicates that RCI differs ($P < 0.05$) among species at that nitrogen level.

Pseudoroegneria and *Festuca*, probably would not sufficiently suppress *Centaurea* to decrease the potential for invasion.

Advantages of the competitive method over herbicides and biocontrol treatments used to manage *Centaurea* are its long duration and low environmental impact. Given these advantages, exclusion of *Centaurea* with *Bromus* merits trial in environments where the danger of invasion exists.

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INDICATORS OF RED SQUIRREL (*TAMIASCIURUS HUDSONICUS*) ABUNDANCE IN THE WHITEBARK PINE ZONE

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ABSTRACT.—We investigated occupied squirrel middens and squirrel sightings and vocalizations as indicators of red squirrel (*Tamiasciurus hudsonicus*) abundance in the high-elevation whitebark pine (*Pinus albicaulis*) zone. Data were collected 1984–1989 from line transects located on 2 study sites in the Yellowstone ecosystem. We evaluated the performance of each measure on the basis of precision and biological considerations. We concluded that, of the 3 measures, active middens were the best indicator of red squirrel abundance. We also observed that the density of active middens dropped by 48%–66% between 1987 and 1989, following a severe drought and extensive wildfires that burned one of the study sites during 1988.

Key words: transect, Fourier series, midden, vocalization, sighting, wildfire.

Whitebark pine (*Pinus albicaulis*) seeds are an important bear food that affects the survival and fecundity of grizzly bears (*Ursus arctos*) in the Yellowstone ecosystem. Use of pine seeds by grizzlies is almost entirely contingent upon the availability of cones cached in middens (i.e., larder hoards) by red squirrels (*Tamiasciurus hudsonicus*). Management of whitebark pine habitats for grizzlies has thus become contingent upon management of red squirrel populations (Mattson and Reinhart 1994).

We studied red squirrels in the whitebark pine zone using data collected from line transects. Because these data included counts of middens, animals, and vocalizations, we were able to evaluate the relative efficacy of these 3 indicators of squirrel presence. We were interested in identifying a "well-behaved" and relevant indicator of density to facilitate our investigation of relationships between squirrel abundance and environmental factors such as midden use by grizzly bears. We were also interested in providing managers with an approach they could use to indicate squirrel abundance, short of using intensive methods that relied upon marked animals.

STUDY AREA

Our study area consisted of 2 sites, one located on the Mt. Washburn massif in north central Yellowstone National Park (44°47′N), and the other near Cooke City, Montana, immediately northeast of the park (45°00′N). These sites spanned the whitebark pine zone, from 2360 to 2870 m elevation. The whitebark pine zone borders upper timberline and is accordingly cold (average annual temperatures <0°C), often windy, and subject to deep (1–2 m) winter snow accumulations (Weaver 1990).

MATERIALS AND METHODS

Broad study objectives affected our transect design. We mapped the study area by habitat type-cover type strata based upon ground-truthed interpretation of 1:20,000 aerial photography. The result was a fine-scale mosaic, with individual map polygons (forest stands) sometimes as small as individual squirrel territories. To minimize effects of edge between different habitat types, we placed transects so as to maximize the number of right-angle intersections with stand boundaries as well as the amount of intersection with stand interiors. Because of this consideration and because forest and meadow were variously intermixed, transect lines were of unequal length.

We surveyed transects in the same order each year, beginning after 10 August and ending prior to 28 September. Two observers walked permanently marked transect lines, with one observer primarily responsible for observations and the other primarily responsible for recording data and keeping on line. At least one of the observers (the junior author) was the same during all years at both sites. Vocalizations and observed squirrels or middens (both active and inactive, by criteria of Finley [1969]) were recorded along with their estimated perpendicular distances from the transect line. Individual cone caches were not considered to be a "midden" and were easily distinguished from these larger, more permanent features.

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We used the computer program TRANSECT (Burnham et al. 1980) to estimate densities. Individual transects constituted sample units for density calculations. As recommended by Burnham et al. (1980), we used the Fourier series, with 1–4 terms, to estimate distance-to-line probability detection functions (g[x]). The distance at which we specified the limits of detectability for our measures (i.e., the cut-point) exerted considerable influence on the fit of the Fourier function to the observed detection distribution. Accordingly, we varied cut-points to achieve the best fit to each year- or site-specific data set. Because data were collected from only 35 transects on the Mt. Washburn massif during 1984 and from 15 transects in the Cooke City area during 1984 and 1989 (compared to 57 and 21 transects, respectively, for all other years), we also calculated densities solely from these original 35 and 15 transects for all years so as to allow comparison with results from 1984.

RESULTS

We sampled the study area 5 yr, 1984–1987 and 1989. During 1988 wildfires burned 562,000 ha of the Yellowstone area, including 52% of the Mt. Washburn transects (47% severely). Transects on the Mt. Washburn area totaled 18.9 km during 1984 (mean transect length [$\bar{X}$] = 539 ± 245 m [s]) and 29.8 km during the remaining 4 yr ($\bar{X}$ = 523 ± 258 m). Similarly, during 1984 and 1989 transects on the Cooke City area totaled 16.4 km ($\bar{X}$ = 1091 ± 427 m) and 21.1 km during the remaining years ($\bar{X}$ = 1005 ± 405 m). We recorded 124 squirrel sightings, 641 vocalizations, and 300 active middens on the Mt. Washburn study site and 54 sightings, 528 vocalizations, and 201 active middens on the Cooke City study site during the 5 study years. The small number of sightings from the Cooke City site prevented us from estimating annual densities from this measure for this area.

Total distance-to-line frequency distributions for each of the 3 measures did not differ between the Mt. Washburn and Cooke City study sites (Mantel-Haenszel χ^2 for ordinal categories, P = 0.51, 0.61, and 0.35 for active middens, vocalizations, and sightings, respectively). Perpendicular distributions of sightings and active middens peaked in the nearest (<10 m) distance category, although the distribution of sightings more closely resembled a negative exponential and the distribution of middens a negative sigmoidal function. The majority (65% and 78%, respectively, by year and study site) of both these distributions were adequately fit (χ^2 test, P > 0.10) by a single-term Fourier function. Distributions of vocalizations peaked in the 2nd (11–20 m) distance category and were characteristically (94%) fit by a 2- or higher-term Fourier function. In 3 (18%) instances we could not achieve an adequate fit by any model.

Relationships among annual density estimates from the 3 measures were varied (Fig. 1). On the Mt. Washburn site, mean sighting and vocalization densities were weakly correlated (r = 0.722), but tended to have overlapping 95% confidence intervals. Only 2 of 9 confidence intervals for the observed estimates (all years, for both the 1984 and inclusive samples) did not contain the line describing perfect correspondence (Fig. 1d). In all but a single instance (Cooke City, 1984), mean midden densities were greater than mean densities of the other 2 measures and were more strongly correlated with sightings than vocalizations (r = 0.981 versus r = 0.831, respectively, for transects 1–57, Mt. Washburn; Fig. 1c). However, in this case, only two of nine 95% confidence intervals for midden and sighting densities included the possibility of perfect correspondence.

CONCLUSIONS

From these results we concluded that densities calculated from active middens were more useful than densities calculated from the other 2 measures for indicating red squirrel abundance. Our conclusion followed from the greater apparent detectability of middens compared to the squirrels themselves, the consistency with which a single-term Fourier function described

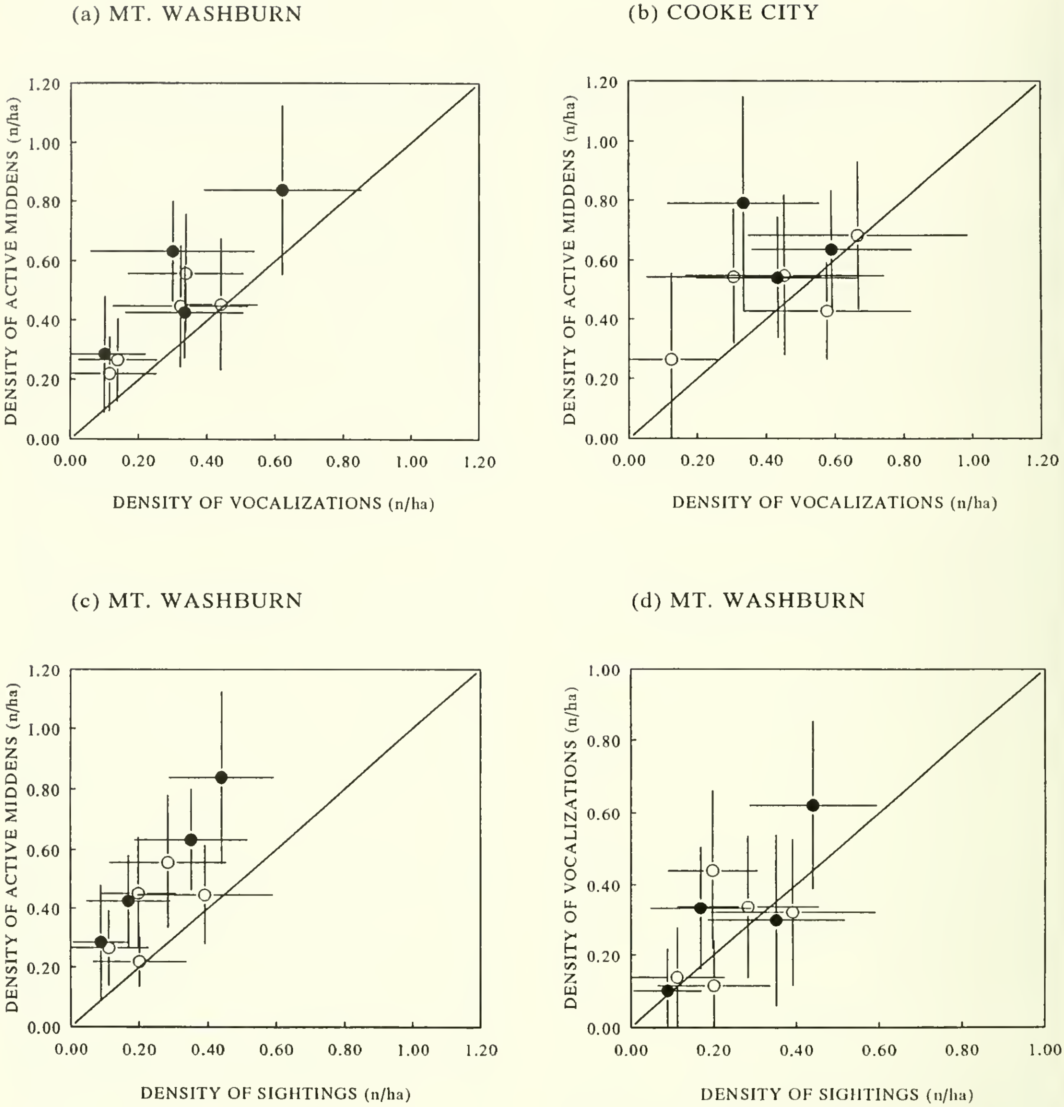

Fig. 1. Relationships between annual estimates of density for active middens compared to vocalizations, (a) for Mt. Washburn and (b) for Cooke City, (c) sightings compared to active middens for Mt. Washburn, and (d) sightings compared to vocalizations, Mt. Washburn, 1984–1987 and 1989. Error bars correspond to 95% confidence intervals, solid circles to results from all transects, and open circles to results from the fewer transects established and first surveyed in 1984. Diagonals represent perfect correspondence between estimates.

the probability detection distribution for middens, and the resulting consistently smaller standard errors for the density estimates. In addition, scatter plots showed that active midden densities tended to be >0 when sighting and vocalization densities were not. By implication, vocalization and especially sighting densities were more likely to underestimate true squirrel densities; i.e., at the same time that active middens clearly indicated the presence of squirrels, sightings and vocalizations could suggest there were none.

Because red squirrel middens are nonmobile, often numerous, relatively easily observed, and typically associated with only one squirrel (Kilham 1954, M. Smith 1968, Wolff and Zasada 1975, Vahle and Patton 1983), they are logical indicators of squirrel abundance. Furthermore, they do not suffer from sampling problems associated with weather, season, and time of day

TABLE 1. Estimated mean (n ha^{-1}) and standard error ($s_{\bar{x}}$) for densities of active middens on the Mt. Washburn and Cooke City study sites, 1984–1987 and 1989, percent coefficient of variations for annual variation 1984–1987, and percent decline in density from 1987 to 1989. Results are given for the transects established and surveyed during 1984 (1–35 and 1–15) and for the larger sample of transects surveyed during all other years, except for 1989, in the Cooke City area (1–57 and 1–21).

	Mt. Washburn				Cooke City			
	Trans. 1–35		Trans. 1–57		Trans. 1–15		Trans. 1–21	
Year	Mean	($s_{\bar{x}}$)	Mean	($s_{\bar{x}}$)	Mean	($s_{\bar{x}}$)	Mean	($s_{\bar{x}}$)
1984	0.447	(0.083)	—		0.428	(0.077)	—	
1985	0.557	(0.110)	0.632	(0.084)	0.682	(0.116)	0.635	(0.095)
1986	0.219	(0.042)	0.426	(0.078)	0.548	(0.126)	0.540	(0.098)
1987	0.453	(0.093)	0.838	(0.143)	0.514	(0.103)	0.790	(0.170)
1989	0.234	(0.062)	0.285	(0.098)	0.262	(0.137)	—	
CV								
1984–1987	35.4		32.6		18.9		19.2	
% decline								
1987–1989	48.3		66.0		51.8		—	

to the same extent as do sightings and vocalizations (cf. C. Smith 1968, Pauls 1978, Ferron et al. 1986). These expectations were corroborated by our analysis. Middens also have a direct tie to management of resources, such as bears, that are of common concern in this zone.

Densities of active middens in our study area averaged between 0.2 and 0.8 ha^{-1}, and on both study sites were lowest during 1989, following the drought and wildfires of 1988 (Table 1). Although annual variation tended to be greater on the Mt. Washburn site compared to the Cooke City site, this difference was not statistically significant (d.f. = 4/4, $F = 1.31$, $P > 0.5$). Both sites exhibited similar annual patterns of variation, including relatively low densities during 1984 and 1986 and a substantial decline in active midden densities between 1987 and 1989.

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THERMAL CHARACTERISTICS OF MOUNTAIN LION DENS

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ABSTRACT.—We used radiotelemetry and searched with a trained hound to locate the dens of 3 recently parturient mountain lions (*Felis concolor*). These dens were located in dense riparian vegetation along the same stream in the bottom of a steep canyon. We monitored the circadian temperatures of 2 dens at 1-h intervals and compared them to ambient temperatures recorded simultaneously. We found mountain lion dens to effectively moderate high ambient temperatures, but these dens failed to provide a thermal advantage at the lowest ambient temperatures recorded in this investigation. We conclude that mountain lion dens provide effective protection from thermal maxima for young, immobile kittens.

Key words: Felis concolor, *mountain lion, temperature, California, den, behavior.*

Female mountain lions (*Felis concolor*) select protected locations in which to bear young (Shaw 1989:7, Beier et al. 1995), but little information is available on den site characteristics for this elusive felid. Here, we describe some characteristics of 3 dens used by different females and their litters and quantify the thermal characteristics of 2 of those dens.

DESCRIPTION OF STUDY AREA

Our study area is located in Mono Co., California, approximately 35 km NW of Bishop (118°25′W, 37°20′N), Inyo Co., California. This area is on the western edge of the Great Basin, immediately east of the crest of the Sierra Nevada. The dominant vegetation type in the general area is sagebrush (*Artemisia tridentata*) scrub with pinyon pine (*Pinus monophylla*) forest at higher elevations. Dense vegetation, dominated by willows (*Salix* spp.) and wild rose (*Rosa* spp.), occurs along the major water courses.

METHODS

During August and September 1994 and 1995, telemetry indicated that several adult females in our investigation of mountain lion ecology had restricted their daily movements. These females returned repeatedly to the same locations, suggesting that they had established natal dens (Beier et al. 1995). We searched these 3 areas and, after detecting vocalizations of neonatal mountain lions, we used a trained hound (Bruce 1918) to locate the dens and kittens. We estimated the ages of these kittens according to criteria summarized by Anderson (1983:43) and Currier (1983).

We examined the thermal characteristics of the dens by placing a recording thermograph (model RTM, Ryan Instruments, Inc., Kirkland, WA) on the floor of each den and an identical instrument on the ground ≤ 100 m away, on a north exposure supporting sagebrush and pinyon pine. Because of the shrubs and trees present on these north-facing slopes, thermographs were not exposed directly to the sun for most of each day. Hourly temperatures were recorded at den 2 from 4 September to 4 October 1994, and at den 3 from 11 August to 16 September 1995; we did not have access to thermographs during the period that den 1 was active. We made ocular estimates of tree height and canopy closure, as well as horizontal cover, at each den.

We used analysis of variance and analysis of covariance to explore the effects of day and time on temperature, simple linear regression to examine the relationship between day of the study and daily temperature, and *t* tests to compare den temperatures with ambient temperatures (Zar 1984).

RESULTS

Three dens containing kittens were located along the Owens River: den 1 contained 1 male and 1 female; den 2 contained 3 males and 1 female; den 3 contained 2 males and 1 female.

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We estimated the kittens at dens 1 and 3 to be ≤ 20 days of age, and those at den 2 to be ≤ 10 days old.

All 3 dens were located in dense groves of willows that ranged in height to approximately 4 m. Wild rose was abundant at all 3 sites, and each den was located ≤ 50 m from the river. Canopy closure at each den was nearly 100%, and direct sunlight did not reach the substrate during any of our midday visits ($n = 2$, den 1; $n = 5$, den 2; $n = 3$, den 3). Horizontal cover at each location was sufficiently dense that, even while standing, we were totally obscured from each other's view at ≤ 3 m. The substrate of all 3 dens was littered with deciduous leaves as well as tree trunks, branches, twigs, and bark. We were able to reach the kittens only by crawling into the dense vegetation present at each site.

We found significant differences between the dens in mean ambient temperature ($\bar{x}_{\text{den } 2} = 13.18 \pm 9.94$ [s]° C; $\bar{x}_{\text{den } 3} = 20.47 \pm 10.61$° C; $F = 202.584$, df = 1, 1630, $P < 0.001$), mean den temperature ($\bar{x}_{\text{den } 2} = 6.01 \pm 5.77$° C; $\bar{x}_{\text{den } 3} = 15.22 \pm 7.08$° C; $F = 807.949$, df = 1, 1630, $P < 0.001$), and mean daily temperature differential (ambient temperature − den temperature; $\bar{x}_{\text{den } 2} = 7.16 \pm 6.05$° C; $\bar{x}_{\text{den } 3} = 5.25 \pm 6.09$° C; $F = 40.224$, df = 1, 1630, $P < 0.001$). At den 2, there was a significant effect of day on ambient temperature ($F = 3.814$, df = 30, 713, $P < 0.001$), den temperature ($F = 3.191$, df = 30, 713, $P < 0.001$), and temperature differential ($F = 4.320$, df = 30, 713, $P < 0.001$). At den 3, however, there was no such effect on ambient temperature ($F = 0.421$, df = 36, 851, $P = 0.999$), den temperature ($F = 0.535$, df = 36, 851, $P = 0.989$), or temperature differential ($F = 0.488$, df = 36, 851, $P = 0.995$). As the study progressed, there was a significant decline at den 2 in ambient temperature ($r = -0.340$, $P < 0.001$), den temperature ($r = -0.112$, $P < 0.001$), and temperature differential ($r = -0.228$, $P < 0.001$); lesser declines in ambient temperature ($r = -0.100$, $P < 0.001$), den temperature ($r = -0.051$, $P = 0.001$), and temperature differential ($r = -0.048$, $P < 0.001$) occurred at den 3.

At both dens, there was significant diel variation in ambient temperature (den 2: $F = 103.382$, df = 23, 720, $P < 0.001$; den 3: $F = 618.443$, df = 23, 864) and den temperature (den 2: $F = 91.008$, df = 23, 720, $P < 0.001$; den 3: $F = 431.275$, df = 23, 864, $P < 0.001$). When date was used as a covariate to control for daily solar radiation, the mean temperature differential also varied on an hourly basis at both dens (den 2: $F = 112.271$, df = 23, 719, $P < 0.001$; den 3: $F = 329.936$, df = 23, 863, $P < 0.001$). Hourly ambient temperatures were greater than corresponding den temperatures at both locations (den 2: $t = 32.285$, df = 743, $P < 0.001$; den 3: $t = 25.662$, df = 887, $P < 0.001$); this difference was especially pronounced at high ambient temperatures (>31° C [HAT]; Fig. 1). At HAT, the temperature differential at den 2 ($\bar{x} = 21.92 \pm 4.49$° C) was >3 times that at moderate ambient temperatures (≤ 31° C [MAT]; $\bar{x} = 6.03 \pm 4.46$° C), and the temperature differential at den 3 ($\bar{x} = 13.56 \pm 8.37$° C) at HAT was nearly 5 times that at MAT ($\bar{x} = 2.87 \pm 3.50$° C). At den 2, the mean range of daily ambient temperatures ($\bar{x} = 28.96 \pm 7.81$° C) was nearly double that of daily den temperatures ($\bar{x} = 15.79 \pm 5.26$° C) ($t = 15.83$, df = 30, $P < 0.001$). Similarly, at den 3 the mean range of daily ambient temperatures ($\bar{x} = 32.54 \pm 3.71$° C) was >1.5 times that of daily den temperatures ($\bar{x} = 20.89 \pm 3.50$° C; $t = 15.24$, df = 36, $P < 0.001$). For both locations combined, den temperatures were less than ambient temperatures for all but 2 (<0.2%) of the paired hourly observations.

DISCUSSION

These mountain lion dens effectively moderated high ambient temperatures, consistent with the hypothesis of Shaw (1989) that dens play an important role in protecting young, defenseless kittens from thermal maxima. At HAT, mean temperature differentials were 3–5 times greater than at MAT (Fig. 1). There were significant effects of time of day (both dens) and day length (den 2) on temperature differential and, hence, the moderating influence of the dens. Nevertheless, den temperatures were less variable than were ambient temperatures. We found no evidence that these dens provided a thermal advantage (i.e., den temperatures greater than ambient temperatures) at the minimum ambient temperatures we recorded; dens may, however, provide protection for kittens when temperatures fall below those that we encountered.

Few descriptions of mountain lion dens are available, but females may select caves, rocky areas, or dense thickets in which to bear young

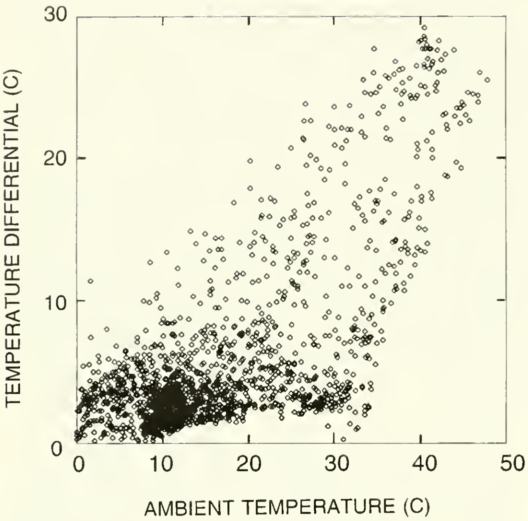

Fig. 1. Mean temperature differential (ambient – den) is more than 3 times greater at high ambient temperatures (>31° C) than at moderate ambient temperatures (≤31° C; data from dens 2 and 3 combined, $F = 1, 241.07$, df = 1, 1630, $P < 0.001$). Mountain lion dens in dense vegetation effectively moderate extreme high temperatures and afford young, helpless kittens protection from ambient maxima, consistent with the hypothesis of Shaw (1989).

(Bruce 1918, Young and Goldman 1946, McBride 1976, Russell 1978, Shaw 1989). We hypothesize that thermal characteristics vary among types of dens, and that mountain lions inhabiting particular environments select den sites based, in part, on the thermal advantage(s) they provide.

In an area with a warm, Mediterranean climate, Beier et al. (1995) reported 2 dens that were located in a small canyon with very heavy cover of "brush," similar to those we investigated. Dens located in thick, woody vegetation may conceal young that are vulnerable to predation, but they also provide protection for kittens from extreme temperatures associated with direct insolation. Such locations provide important thermal benefits for kittens at high ambient temperatures, and a more stable thermal environment than exists outside the den throughout the range of ambient temperatures we recorded. Movements by kittens for thermoregulatory purposes might be lessened under these circumstances. Fewer movements by kittens may decrease the probability of discovery by potential predators, thereby enhancing the survival of young, defenseless mountain lions.

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JAMES WILLIAM BEE
1913–1996

Wilmer W. Tanner[1]

James W. Bee

James W. Bee, professor of zoology and emeritus, University of Kansas, Lawrence, Kansas, died at Seattle, Washington, 18 April 1996. He was born 25 September 1913 in Provo, Utah. His family, including parents, Robert G. and Mary Culbertson Bee, and brother and sister, Max and Mary, were residents of Provo, Utah, where they received their early education. It was from this setting in Utah Valley that James was introduced at an early age to the sciences of archaeology and ornithology by his father, who loved natural history and the little-known history of Utah Valley, its lake, and its early inhabitants.

As a youth and young man, he accompanied his father on many collecting trips that resulted in assembling artifacts of the past. These archaeological finds provided valuable information pertaining to Indian winter camps, summer camping areas, and burial grounds, and an insight into the role of Utah Lake and the surrounding mountains as providers of abundant fish and game.

Their travels near this lake and in the mountains brought them in contact with numerous birds. Each spring flocks of birds entered the valley—some remained and others moved on. This phenomenon stimulated a great interest, so much so that James, his father, and various friends became amature ornithologists. Their ornithological work encompassed life history studies, observation of arrivals in the spring, and investigation of nests and nesting. Ultimately, this interest in birds lead to the assembly and preparation of eggs for those species nesting in the valleys and mountains of central Utah.

Thus was born a naturalist whose contributions are invaluable and most of which could not now be assembled. The archaeological collections are presently at the Museum of Peoples and Cultures, Brigham Young University. James and his father contributed 812 sets of bird eggs and 112 single eggs representing 234 species. James contributed 7918 mammal, 245 bird, and 504 amphibian and reptile specimens to the M. L. Bean Life Science Museum, also at Brigham Young University. In the Bean Museum Library are field records, 27 volumes from James and 20 volumes of his father's, all well documented and done with great care. These were written in the field as the data were obtained and represent field records of a time when some pristine conditions still existed.

James entered Brigham Young University in 1932 and received his B.A. degree in 1937. World War II interrupted his studies for the M.A., but this he finished in 1947. As an undergraduate, he became interested in and researched mammals. Thus his master's research was the mammals of Utah County. While in the Armed Forces (1941–1946), he was trained as a hospital administrator and served as a sergeant-major, organizing 50 key men as a cadre to establish a new hospital. He supervised several new hospital departments and for a year and a half served in field hospitals for airborne units in India, Assam, Burma, and China. During these years he met Annette P. Malseed, R.N. They were married 15 October 1945 in Kunming, Yeaman, China.

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In September 1948 James entered the University of Kansas to continue his research in mammalogy, with a desire to complete his study on the genus *Microtis.* He completed his studies at KU and spent a summer at Friday Harbor, Washington. He was a noted field zoologist and spent many years collecting research material and field data for the Museum of Natural History at the University of Kansas. Students doing research in vertebrate zoology at Brigham Young University or at the University of Kansas will find numerous specimen tags labeled "collected by James Bee." After 37 years he retired from KU and built a new home on Lopez Island, Washington. James and Annette were the parents of three children: James Robert, Annette Christine Kenagy, and Mary Pauline Bee Kaufman.

It was my pleasure to have spent several summer field trips with James. A highlight was the summer of 1939 when we studied the vertebrates of western Utah County. During this time we prepared and assembled museum specimens; of importance to me was finding a nesting colony of the western skink and securing additional specimens of *Hypsigalena.* We both participated in the new discoveries, and it was obvious that Jim was at his best in preparing precise field data. I learned much from him that summer and appreciated his dedication to a complete understanding of the natural world we were investigating.

James had a very likeable personality that was reflected in his family, which he held in high esteem.

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BROOK STICKLEBACK (*CULAEA INCONSTANS* [KIRTLAND 1841]), A NEW ADDITION TO THE UPPER COLORADO RIVER BASIN FISH FAUNA

Timothy Modde[1] and G. Bruce Haines[1]

Key words: brook stickleback, range extension, nonnative.

Brook stickleback (*Culaea inconstans*) is a small gasterosteid fish native to Arctic and Atlantic drainages in North America. The species native range extends west from Nova Scotia to British Columbia and south from the Northwest Territories to southern Ohio drainages, including the Mississippi-Missouri River above the confluence of the Illinois River (Scott and Crossman 1973). Hubbs and Lagler (1958) reported brook stickleback from the Illinois River in Illinois and the Missouri River in Kansas. Historical accounts exist of relictual populations in the Platte River system, but Cross (1967) noted its absence from Kansas. An isolated, and presumably relict, population occurs in the Canadian River drainage of New Mexico (Koster 1957). Brook stickleback has been collected outside its native range in Alabama (Boschung 1992), Kentucky (Burr and Warren 1986), Tennessee (Etnier and Starnes 1993), the Rio Grande River drainage in New Mexico (Sublette et al. 1990), Colorado (Zuckerman and Behnke 1986), and the Klamath River, California (Peter Moyle, University of California, Davis, personal communication).

Between July and October 1995 we collected 5 brook stickleback from the middle Green River, Uintah County, Utah, the 1st record for the species in Utah (catalog number LFL 24871, Larval Fish Laboratory, Colorado State University). Brook stickleback was first reported elsewhere in the upper Colorado River drainage in 3 small tributaries of the Elk River (South, Coleman, and Deep creeks) in northwestern Colorado in 1993 (Jake Bennett, Colorado Division of Wildlife, personal communication).

One brook stickleback juvenile, 27 mm total length (TL), was collected 18 July 1995 in a quatrefoil light trap at the outlet of Old Charley Wash, river kilometer (RK) 402 on the Green River (RK measured from the confluence of the Green and Colorado rivers). Four adult fish, (41, 46, 48, 54 mm TL) were collected between 1 October and 12 October 1995 from Old Charley Wash, a wetland on the Ouray National Wildlife Refuge that connects to the Green River during high spring flows. Fish were collected when the wetland was drained (Modde in press); all were found in low or no velocity habitats.

Tyus et al. (1982) cited the establishment of 42 nonnative fishes in the upper Colorado River compared to 13 native species. Brook stickleback is an additional transplanted species, probably the result of human introduction rather than a natural range extension. Brook stickleback introductions elsewhere in the United States were presumably through bait bucket transfers or contaminated game fish stockings (Zuckerman and Behnke 1986, Sublette et al. 1990).

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ERRATA

Correction to:

Sutherland, Steven D., and Robert K. Vickery, Jr. 1993. On the relative importance of flower color, shape, and nectar rewards in attracting pollinators to *Mimulus*. Great Basin Naturalist 53: 107–117.

The article states: "Hummingbirds are commonly said to have evolved a preference for red or orange-red flowers," citing (1) K. A. Grant, 1966, A hypothesis concerning the prevalence of red coloration in California hummingbird flowers, American Naturalist 100: 85–98; and (2) K. A. Grant and V. Grant, 1968, Hummingbirds and their flowers, Columbia University Press, New York, 115 pp., among other references. In fact, the Grants point out just the opposite, i.e., that experimental investigation shows that hummingbirds have not evolved a preference for red or any other color. Actually, Sutherland and Vickery's article comes to this conclusion also.

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BOOK REVIEW

Snakes of Utah. Douglas C. Cox and Wilmer W. Tanner; Mark Philbrick, photography. Monte L. Bean Life Science Museum, Brigham Young University, Provo, UT. 1996. $17.95 softcover.

Snakes of Utah, anticipated for some time, is finally available for distribution. This booklet (92 total pages) includes all known species and subspecies of snakes found in the state, with brief descriptions, habits, and habitats, along with colored photographs of each. While most people will likely shudder at the thought of snakes, especially while viewing photographs, the enthusiast will recognize the value of the illustrations and other published information. Generally, the booklet is written in nonscientific language, but it also includes some scientific notations. For instance, scientific names and authorities of the 33 species and subspecies, along with common names, are included for each. Of interest (perhaps only to the specialist) is the fact that only 2 binomials are found among all Utah snakes; 31 are trinomials. It might be concluded that, because of subspeciation, only 27 kinds of snakes are found in Utah. To the general public, a night snake is a night snake, a garter snake is a garter snake, and a rattlesnake is a rattlesnake. Herpetologists have named subspecies for practically all snakes, compounding one's knowledge of these animals. Technically, where closely related subspecies show sympatric distribution, there should be intergradation between the 2 types. Most individuals using this booklet will probably not recognize differences between related subspecies found especially in these sympatric regions. If intergrades are not present, then these should be elevated to species and not kept as subspecies. Little information is found in the booklet on intergradation of characteristics.

An important contribution of this booklet is the colored photographs. While not captioned, most photographs are obvious because they are shown on the page opposite the name and other information on that snake. This publication would be more useful if a caption were shown by the other photographs throughout the text, e.g., the photo opposite page 1 and those shown on pages 3, 4, 5, 8. The herpetologist will probably recognize these without caption, but, as stated, it's likely these specialists will not be the primary users of the text. Identification of snakes by these photographs may not be obvious to most readers. Most photos show colors and patterns of snakes, but a few, such as the full view of the Upper Basin garter snake on page 59, do not show these identifiable features. It's interesting that the only snake not represented by a photo of the entire body is the Sonoran lyre snake on page 67. One wonders why. Perhaps it's because this snake is "considered to be rare." However, the Dixie College Natural Science Museum contains records of 7 specimens, 2 having been found in what is now considered "downtown" St. George, 1 specimen as recently as 1980. It seems likely that with a little effort, one of these "rare" snakes might have been found. The photo of the Utah blind snake on page 17 is a surprise. Of the several dozen blind snakes observed by this writer, representing localities from the Red Cliffs Recreation Area near Leeds, Washington County, to the extreme northwest corner of Arizona, not 1 specimen even approached this dark phase. They have all been a pale tan color, frequently showing a suffusion of pink.

Another important contribution of this booklet is the distribution maps included with each species along with the general and sometimes specific distribution of the snake within the state. While it is difficult to show accuracy on a small map, some maps are erroneous. For instance, the distribution of the Painted Desert glossy snake is "in the extreme southeastern sector of the state, adjacent to northeastern Arizona" (page 40). The map, however, shows it is found more south central than southeastern. An inconsistency from text to map is also observed with the California king snake (page 46). If this snake occurs "from the southwest corner east to the Colorado River," why does the distributional map extend considerably beyond the Colorado River along the San Juan River? Nothing in the text is speculative of a range extension. The maps of the Utah mountain king snake (page 48) and the Utah milk snake (page 50) do not accurately depict their known distributions in Washington County. On page 60, of the western blackneck garter snake, the text states "its northernmost habitat is associated with streams . . . in the regions of southeastern Utah." The map shows its distribution into east central Utah. Reference is made to a ground snake having been collected in Carbon County, far from its known range, and this area is shown on the map. Might this specimen have been one that escaped or was released from captivity? (Reports have been made of individuals transporting this snake from the St. George area, where it is common, to elsewhere in the state.) There is speculation that the Utah blackhead snake "may occur further north in Emery and Carbon Counties." (The proposed expansion is not shown on the map.) Why might it not, then, be found in Wayne County and perhaps even San Juan and Grand counties? If the midget faded rattlesnake is found at Flaming Gorge, why does the map not show distribution in that area?

While it would add to the length of the text, it would have been better had the authors given complete distribution ranges for all species and subspecies, rather than just a few. A snake doesn't recognize a political boundary as being its limits! However, it could be reasoned, if the distribution extends to the Utah boundary, the occurrence of that snake would also be in the neighboring state.

The full-page map of the state of Utah (page 11) is a good addition to the text. However, with the number of snakes found only in Utah's Mojave Desert, this feature might have been identified along with the others. In the geographical and ecological descriptions of Utah (pages 9–10), considerable discussion is given about montane regions, some at high elevations, yet little is written about the low, hot desert or the higher, cold desert, although the authors admit to the richness of reptile fauna, especially in the low, hot desert, the southwestern region of the state.

In addition to these other features, *Snakes of Utah* includes both glossary, though not inclusive of all technical words used in the text, and index.

The writer wonders at the importance of the full page of illustrations (page 13) showing scalation with so little reference to most of these features in descriptions. Some of these features are referenced; most are not.

While full pages of color separate groups of snakes, does this mean that Joshua trees are characteristic of the distribution of the Utah blind snake? Although the illustration on page 18 may be typical of the habitat of the rubber boa in Utah, and on page 72 of the habitat of some of the rattlesnakes, does the illustration on page 22 depict the typical distribution of the colubrids? Perhaps these "division pages" were added merely for color; nevertheless, they are attractive.

The authors of the booklet include a number of interesting anthropomorphisms, perhaps intentionally. Some of these are noted: (1) In the introduction, the statement is made (page 5) that "the snake employs rocks and brush to snag the skin and hold it while the snake crawls out." One wonders if the snake does this intentionally. (2) "Denning is a behavior pattern that provides the snake with an opportunity to come in contact with other snakes of the same species" (page 6). (3) Of the rubber boa, "it will often cling like a bracelet and seem to enjoy it as much as the person" (page 20). (4) The statement is made about the western yellowbelly racer (page 28) that "it will attempt to bite if it feels at all threatened." (5) Another example is that rattlesnakes use the rattle "as a warning device to intimidate other animals that may harm the snake" (page 75).

Miscellaneous errors or inconsistencies in narrative, grammatical or otherwise, are found. The introduction, for instance, discusses tall tales and folklore of the American West. This booklet is, of course, about snakes of one region of the American West, but tall tales and folklore—even some of the same stories heard in the American West—are repeated wherever snakes are found.

On pages 4 and 5 the statement is made that "the mouth is the most universally used weapon employed by snakes in self-defense." The emphasis is obvious because the accompanying text is about self-defense, but snakes use their mouths more often as a means of obtaining food. Also, in the introduction, the statement is made that "these studies and *our museum program* help them to understand." (page 6, emphasis added). Later in the text (page 9) reference is made to Brigham Young University's Monte L. Bean Life Science Museum. The complete identification of the museum should have been made when it was first referenced on page 6. It could be pointed out, too, that other schools and museums might have the same purpose—to "help them to understand" about snakes.

While the following is not necessarily in error, it reflects a writing style. On page 12 the following statements are made: "These snakes do not pose any threat to man but they do provide a mild venom to help immobilize their prey. Their prey includes worms, insects, frogs, lizards, and small mammals." In writing, repeated words and phrases should be avoided in consecutive sentences or within the same sentence. It could better have been written, "to help immobilize their prey, which includes worms, insects. . . ."

In the introduction to the tropical wormlike snakes, the statement is made that "they feed on insects and worms, especially termites and ants, found in the soil." The emphasis in this statement suggests that termites and ants are kinds of worms. This should have been written, "they feed on worms and insects, especially termites and ants." In reference to the Utah blind snake the statement is made (also on page 15) that Vasco M. Tanner "had seven specimens to examine, and the name is based on No. 662 in the BYU type collection." *Name* is inappropriately used, although specimen No. 662 might have been published as the type specimen.

One of the most frequently made grammatical errors in writing is the inconsistency of singulars and plurals within a sentence. On page 20, this type of error is made. The rubber boa "is a delightful animal to have around their wrist." Inasmuch as *their* is plural, the plurality of *wrists* must also be used.

Reference is made twice (on pages 30 and 44) that the snakes occur on "the margins of deciduous forests." Small groups of deciduous trees may occur in riparian areas or where trees are cultivated, but technically, deciduous forests do not occur in the state of Utah.

The redundant statement is made about the western leafnose snake that the rostral scale "looks leaflike."

An inconsistency is noted about the Utah mountain king snake and the Utah milk snake. Page 48 states: "If a specimen has a white nose, it is most likely a mountain king snake. If, however, it has a black nose, it is probably a milk snake. These characteristics are *not completely reliable*" (emphasis added). Page 50 states that "the milk snake differs in that it has a black nose."

On pages 68 and 70 the habits of the Mesa Verde night snake and the desert night snake are described as "nocturnal, secretive, and seldom seen." Furthermore, it is stated that the former "feeds primarily on the lizard *Uta stansburiana uniformis* and other small lizards," while the latter "feeds primarily on the side-blotched lizard *Uta stansburiana stansburiana*." One wonders about this inasmuch as lizards are primarily diurnal and snakes nocturnal. Of course, snakes could feed at night while lizards are inactive.

While reference is made in the booklet about the influence of soil on the ground color of some snakes, there is no mention of this occurring in the Mojave Desert sidewinder (page 78). Of the hundreds of sidewinders observed by the author in the past 50 years, the influence of soil color on the ground color of the snake is most obvious.

Despite these criticisms, *Snakes of Utah* should contribute importantly to our knowledge of these reptiles within a limited political region. As noted, the booklet is written for laymen, and its distribution is more appropriate in national and state parks and monuments than in the scientific community. It is a "must" for backpackers, individuals, and families spending time in the out-of-doors where snakes might be encountered. The authors, the photographer, and the publisher are to be commended for finally making this booklet available.

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THE FUTURE OF ARID GRASSLANDS: IDENTIFYING ISSUES, FINDING SOLUTIONS

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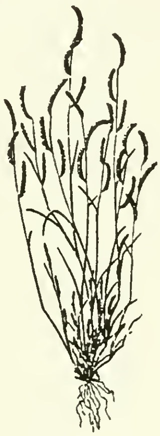

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SPECIES-ENVIRONMENT RELATIONSHIPS AMONG FILTER-FEEDING CADDISFLIES (TRICHOPTERA: HYDROPSYCHIDAE) IN ROCKY MOUNTAIN STREAMS

Timothy B. Mihuc[1,2], G.Wayne Minshall[1], and Janet R. Mihuc[3]

Abstract.—Species-environment relationships were determined for filter-feeding macroinvertebrates from 55 Rocky Mountain stream sites to establish species distribution patterns. Species abundance and 20 environmental variables were measured at each site with species-environment relationships determined using canonical correspondence analysis and stepwise multiple regression. Results suggest that the distribution of several taxa was strongly related to upstream-downstream environmental gradients. *Arctopsyche grandis* abundance increased with stream size (width and depth) and decreased with increasing turbulence (Reynolds number). *Brachycentrus* abundance also increased with stream size (depth). *Hydropsyche* abundance increased with increasing baseflow. *Parapsyche elsis* abundance demonstrated negative correlation with depth, Froude number, and conductivity. Taxa followed previously reported patterns, partitioning habitat according to stream size. *Arctopsyche grandis, Brachycentrus*, and *Hydropsyche* were found in larger (3rd- to 6th-order) streams, while *Parapsyche elsis* was observed in small headwater (1st- and 2nd-order) streams. Other filter-feeding taxa such as *Simulium*, *Pisidium*, and ostracods exhibited little or no apparent habitat partitioning among stream sites.

Key words: species-environment relationships, filter feeders, Rocky Mountain streams.

Benthic macroinvertebrates adapted for removing particles from suspension (filter feeders) are an important component of stream communities. Distribution patterns and habitat associations among filterers have been well documented, particularly for members of the Trichoptera family Hydropsychidae (e.g., Décamps 1968, Edington and Hildrew 1973, Gordon and Wallace 1975, Wallace and Merritt 1980, Ross and Wallace 1982, Tachet et al. 1992) and for lake outlet communities (e.g., Robinson and Minshall 1990, Richardson and Mackay 1991). Many studies have determined filterer associations with food resources and environmental factors such as water velocity or temperature (e.g., Edington 1968, Wallace 1974, Haddock 1977, Wallace and Merritt 1980, Alstad 1982, Hauer and Stanford 1982, Bruns et al. 1987, Osborne and Herricks 1987, Wetmore et. al. 1990, Voelz and Ward 1992). Few studies have considered the entire filterer component found in natural (unimpounded, unregulated) streams and distribution patterns of filterer species with respect to a wide range of environmental variables (Edington and Hildrew 1973, Gordon and Wallace 1975, Boon 1978, Ross and Wallace 1982). Our objective was to assess the distribution patterns of filter feeders in unimpounded Rocky Mountain, USA, streams to determine relationships with specific environmental variables including flow parameters; stream size, depth, and width; benthic organic matter content; slope; water chemistry; periphyton biomass; and temperature. While many studies have considered current velocity, temperature, and food relationships, partitioning of habitat by filter feeders in relation to other environmental variables is poorly known.

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METHODS

Stream sites encompassed the Rocky Mountain region from northern Wyoming to central Idaho, including 22 streams in Yellowstone National Park and 33 in central Idaho. Streams ranged from 1st to 6th order in size (Table 1). All sites were unimpounded and none were located below lake outflows. Yellowstone sites were sampled each August from 1988 to 1992. All other sites were sampled between July and September during the year(s) indicated in Table 1. Sampling methods were routine methods used in stream ecology (e.g., Platts et al. 1983). Briefly, benthic organisms were sampled using a surber net (250 micron mesh) in riffle habitat at 5 transects located at 50-m intervals along a stream reach (250 m total reach length). Samples were taken to a depth of 10 cm. Mean density for each filterer species within each stream reach was used in statistical analyses to determine relationships with physical variables. Physical environmental variables measured at each stream reach included stream order, slope, width, baseflow (1 transect), mean depth (n = 100 random measurements), mean water velocity (n = 100 random measurements), mean embeddedness (n = 100 random measurements), and mean substrate size (n = 100 random measurements). Reach-scale means for all variables were used in statistical analyses. Width/depth ratio and several hydraulic parameters (mean Froude number, mean Reynolds number) were calculated from these measurements. Annual stream temperature range was estimated from annual maximum (estimated as temperature at the time of sampling) and minimum temperature (the freezing point of water). Water chemistry variables included hardness, alkalinity, pH, and specific conductance. Other biotic variables measured at each stream reach were chlorophyll a (n = 5 per site), ash-free dry mass (AFDM) of periphyton (n = 5 per site), biomass/chlorophyll ratio of periphyton (B/C), and benthic organic matter content (BOM; n = 5 per site). This study did not address food resources or food acquisition among filter feeders; therefore sampling of transported and benthic fine particulate material was not included in sampling protocol.

Relationships between species and environmental variables were determined using canonical correspondence analysis (Ter Braak 1986) and stepwise multiple regression. All comparisons were made on reach-scale data (reach means for all variables). Comparisons reflect spatial differences among sites sampled in 1 season (summer) to determine large-scale distribution patterns of filter feeders in 1st- through 6th-order streams. Temporal patterns were not considered here. Canonical correspondence analysis (CCA) allows the investigator to interpret multiple species responses along a gradient of multiple environmental variables. This analysis provides a useful interpretation of species-environment relationships through the resulting ordination plot. Once species-environment correlations were identified using CCA, multiple regression analysis was used to further discern relationships between species abundance and environmental variables.

RESULTS

In the canonical correspondence analysis (Fig. 1) the first ordination axis (x axis) explained 37.9% of the total species-environment relationship and the second (y axis) an additional 30.7% (Table 2). Results indicate that several environmental variables were important in explaining variation in species abundance across sites (Fig. 1). *Arctopsyche grandis* and *Hydropsyche* abundance related directly to increasing baseflow, width, and stream order (Fig. 1). *Parapsyche elsis* abundance was inversely related to increasing baseflow, width, and stream order. *Brachycentrus* abundance related primarily to depth, substrate size, Reynolds number, and annual temperature range (Fig. 1). *Simulium*, *Pisidium*, and Ostracoda abundance

TABLE 1. Summary of the 55 study streams. Sites are arranged by increasing stream order and increasing depth within each order.

Stream	Sample dates	Order	Avg depth (m)	Avg width (m)	Baseflow (m/s)	Slope (%)
Cache, YNP	1988–1992	1	0.06	0.704	0.003	12
E Blacktail Deer, YNP	1988–1992	1	0.13	0.665	0.048	1.7
Twin, YNP	1988–1992	1	0.13	0.643	0.06	10.7
W Blacktail Deer, YNP	1988–1992	1	0.17	0.550	0.043	3.8
Fairy, YNP	1988–1992	1	0.23	0.307	0.066	1.0
Pioneer, ID	1990	2	0.05	0.342	0.13	6
Dunce, ID	1990,91	2	0.06	0.109	0.07	17
Goat, ID	1990,91	2	0.06	0.089	0.05	18
Cache, YNP	1988–1992	2	0.09	0.764	0.012	10.1
Packhorse, ID	1991	2	0.09	0.413	0.04	4
Castle, ID	1992	2	0.09	0.160	0.03	11.5
Yellow, ID	1992	2	0.09	0.220	0.03	8
Rose, YNP	1988–1992	2	0.10	0.416	0.027	7.8
Sliver, ID	1991	2	0.10	0.243	0.04	5
EF Whimstick, ID	1991	2	0.10	0.460	0.02	2
Cache, YNP	1988–1992	2	0.11	0.832	0.012	8.8
Cliff, ID	1988,90,91	2	0.12	0.407	0.18	12
Amphitheater, YNP	1988–1992	2	0.13	1.11	0.146	4.9
Pony, ID	1992	2	0.13	0.380	0.08	13
Iron Springs, YNP	1988–1992	2	0.14	0.237	0.038	13.1
E McCall, ID	1991	2	0.14	0.196	0.05	2
Blacktail Deer, YNP	1988–1992	2	0.15	0.710	0.151	15.2
Fairy, YNP	1988–1992	2	0.18	0.395	0.083	0.26
WF Cave, ID	1990	3	0.05	0.124	0.01	6
Doe, ID	1990	3	0.10	0.316	0.02	16
SF Cache, YNP	1988–1992	3	0.16	1.70	0.195	3.0
Pioneer, ID	1990	3	0.16	0.612	0.31	6
Hellroaring, YNP	1988–1992	3	0.17	1.23	0.32	2.5
McCall, ID	1991	3	0.17	0.196	0.05	2
Pebble, YNP	1988–1992	3	0.18	1.10	0.592	2.5
Cougar, ID	1990,91	3	0.18	0.297	0.10	12
Cache, YNP	1988–1992	3	0.19	4.60	0.475	1.7
Lava, YNP	1988–1992	3	0.24	0.768	0.893	2.1
Iron Springs, YNP	1988–1992	3	0.27	0.587	0.520	1.1
Beaver, ID	1988	3	0.27	0.800	1.17	4
Cache, YNP	1988–1992	4	0.18	2.05	0.67	1.2
Ramey, ID	1988	4	0.18	0.630	0.74	3.5
Boulder, ID	1992	4	0.19	1.23	0.41	2
Hellroaring, YNP	1988–1992	4	0.20	2.61	0.43	1.8
McCall, ID	1991	4	0.22	0.240	0.13	2
Whimstick Main, ID	1991	4	0.23	0.800	0.10	1
WF Rapid, ID	1992	4	0.25	0.930	1.80	3
Lamar, YNP	1988–1992	4	0.34	2.87	2.85	.97
Soda Butte, YNP	1988–1992	4	0.35	2.90	3.00	1.3
Indian, ID	1992	5	0.21	1.43	1.31	1.5
Pistol, ID	1992	5	0.33	1.70	1.80	1.8
Rush, ID	1988	5	0.35	1.51	1.61	1
Camas, ID	1992	5	0.38	2.10	2.92	1
Chamberlain, ID	1992	6	0.24	1.69	2.43	3.5
Big Ck @ Coxey, ID	1988	6	0.31	3.42	5.23	1.5
Rapid, ID	1992	6	0.37	1.48	1.11	2.5
Loon, ID	1992	6	0.37	2.91	3.29	1
Big Ck @ Gorge, ID	1988	6	0.37	4.32	8.83	1
Big Ck @ Rush, ID	1988	6	0.45	4.3	8.04	1.5
Salmon River, ID	1992	6	0.48	1.40	5.47	1

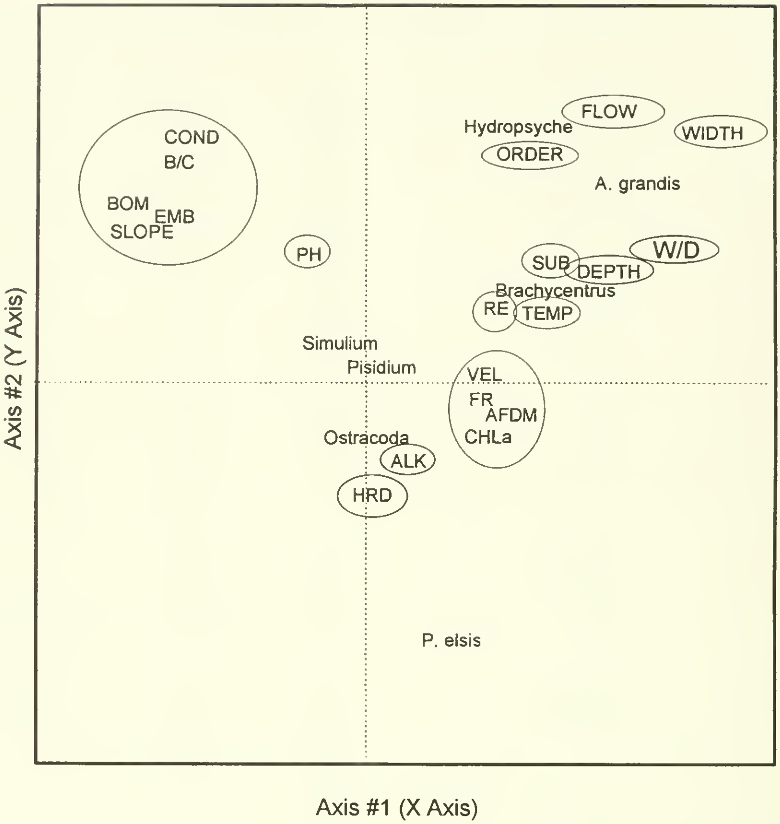

Fig. 1. Biplot results of canonical correspondence analysis. Environmental variables (circled) are listed in Table 3. Species are plotted using species names. Positive abundance relationships with a given environmental variable are indicated by species that fall close in the ordination plot to the environmental variable. Species that fall on the opposite end of the plot from an environmental variable exhibit a negative relationship with that variable. Species near the center of the plot exhibit little relationship with environmental variables.

did not relate to any of the environmental variables in the ordination plot and are not considered further.

Stepwise multiple regression results indicate species-environment relationships similar to those found in the ordination (Table 3). *Arctopsyche grandis* abundance was positively correlated with stream depth and width and negatively correlated with turbulent flow (Reynolds number). *Brachycentrus* abundance was positively correlated with stream depth (Table 3). *Hydropsyche* abundance showed positive correlation with baseflow and negative correlation with water hardness and substrate size. *Parapsyche elsis* abundance showed negative correlation with depth, surface turbulence (Froude number), and specific conductance (Table 3).

DISCUSSION

Our results support the idea that macroinvertebrate species in streams respond to environmental conditions in individualistic ways. Each taxon was related to a different set of environmental variables. General relationships with environmental variables for *A. grandis*, *Brachycentrus*, and *Hydropsyche* suggest that these taxa are adapted for larger river systems (3rd–6th order; Fig. 2). *Brachycentrus* and *Hydropsyche* are usually found in lower reaches in river systems (4th–6th order; Edington and Hildrew 1973, Boon 1978, Hauer and Stanford 1982, Ross and Wallace 1982, Wetmore et. al. 1990). *A. grandis* is most often found in mid-reaches (3rd–5th order; Alstad 1980, Cuffney and Minshall 1981, Hauer and Stanford 1982).

TABLE 2. Results of canonical correspondence analysis. Eigenvalues give the importance of an axis on a scale between 0 and 1. Total inertia is the total variance in the species data. The species-environment correlations scale the strength of the relationship between species and environment for the axes.

Axes	1	2	3	4	Total inertia
Eigenvalues	.444	.360	.174	.085	2.50
Species-environment correlations	.819	.772	.640	.441	
Cumulative percentage of variance:					
of species data	17.8	32.1	39.1	42.5	
of species-environment relationship	37.9	68.6	83.5	90.7	
Sum of all canonical eigenvalues					1.172

Among the taxa adapted for large streams, habitat partitioning is apparent in this study as in others (Edington and Hildrew 1973, Boon 1978, Alstad 1980, Hauer and Stanford 1982, Ross and Wallace 1982). Taxa exhibited reach-scale macrohabitat preferences with *Brachycentrus* distribution related to stream depth, *Hydropsyche* related primarily to stream flow, and *A. grandis* to a combination of width, depth, and turbulence.

P. elsis was prevalent in headwater stream reaches (Fig. 2), a pattern found in several other studies (Alstad 1980, Hauer and Stanford 1982). Distribution patterns for *P. elsis* were explained by flow and stream-size variables. Stream temperature may also be an important variable explaining *P. elsis* distribution patterns (Alstad 1980, Hauer and Stanford 1982). Annual temperature was measured in this study based only on yearly max/min readings, which may not adequately reflect differences in temperature between headwater sites and downstream locations, resulting in the lack of *P. elsis* patterns explained by temperature in our analysis. Also, previous studies that suggest a downstream temperature gradient as the explanation for *P. elsis* distribution (Hauer and Stanford 1982) did not consider other variables (e.g., physical and hydrologic variables) that may contribute to habitat selection by *P. elsis*. Multiple factors are probably responsible for *P. elsis* high abundance in headwater streams, including temperature patterns and hydraulic conditions.

Our results agree with published distribution patterns for all 4 taxa and provide evidence for physical factors that are important in determining habitat selection for each taxon (Fig. 2). Habitat preferences demonstrated in this study are for distribution patterns among streams at the reach scale. Data were collected within a 250-m reach at each site and expressed as reach means for all variables in order to identify factors affecting large-scale (among site) distribution patterns among taxa. Microhabitat requirements are ultimately responsible for the physical habitat selected by filter feeders (Smith-Cuffney and Wallace 1987, Wetmore et. al. 1990), but reach-scale comparisons allow broader scale distribution patterns to be studied. The reach-scale comparisons herein indicate general conditions at each site in terms of available macrohabitat. The trends observed in the data indicate animal preferences for a given reach and its associated habitat conditions. Differences in reach-scale means among variables may also reflect differences in general microhabitat conditions available among sites (e.g., slow- or fast-velocity microhabitats). Reach-scale means, therefore, can serve as a useful integrator of microhabitat conditions in order to facilitate comparisons at larger scales.

Evolutionary patterns probably have led to habitat partitioning based on current speed and filtration rate among filter feeders in Rocky Mountain streams with some taxa adapted for larger streams (*Brachycentrus, Hydropsyche*, and *A. grandis*) and some for smaller systems (*P. elsis*; Alstad 1980, 1982). Filter feeders may be a useful group to address habitat partitioning on large spatial scales in streams because many filterer taxa appear to have partitioned habitat at these scales. In this study, stream size (width, depth) and hydraulic parameters (baseflow, turbulence) were more important in explaining species-environment relationships than other variables such as water chemistry, periphyton biomass, or benthic organic matter. Our results provide support for the idea that evolutionary divergence among benthic macroinvertebrate filterers has resulted in habitat partitioning according to stream size and hydrologic parameters in Rocky Mountain streams

TABLE 3. Summary of the stepwise multiple regression results of the 4 most abundant species (dependent variable) versus the 20 environmental variables. Partial correlation coefficients and p values (parentheses) are shown for each variable. Variables included in the regression model for each species are shown (variable included if $P < 0.05$). Variable acronyms in Figure 1 are shown in parentheses.

Environmental variable	*Arctopsyche grandis*	*Brachycentrus*	*Hydropsyche*	*Parapsyche elsis*
Stream order				
Depth	0.25 (0.004)	0.36 (0.00003)		–0.23 (0.009)
Width/depth ratio (W/D)				
Width	0.18 (0.04)			
Temperature (TEMP)				
Slope				
Embeddedness (EMB)				
Baseflow (FLOW)			0.64 (0.0000)	
Velocity (VEL)				
Substrate size (SUB)			–0.21 (0.019)	
Froude number (FR)				–0.19 (0.031)
Reynolds number (RE)	–0.30 (0.0008)			
Hardness (HRD)			–0.21 (0.018)	
Alkalinity (ALK)				
pH				
Conductivity (COND)				–0.175 (0.049)
Periphyton chl. *a* (CHL a)				
Periphyton AFDM (AFDM)				
Periphyton B/C ratio (B/C)				
Benthic org. matter (BOM)				
Multiple R^2	0.63	0.22	0.59	0.53

(Gordon and Wallace 1975, Boon 1978, Alstad 1980, Hauer and Stanford 1982, Ross and Wallace 1982).

While food resources were not considered in this study, factors such as food type, quality, and particle size are also important in explaining filterer distribution and abundance along stream gradients (Alstad 1980, Cuffney and Minshall 1981, Hauer and Stanford 1982, Ross and Wallace 1982, Richardson and Mackay 1991, Voelz and Ward 1992). According to the shredder-collector facilitation hypothesis, longitudinal distribution patterns among collector-filterers are thought to relate to the generation of fine particulate organic matter (FPOM) by upstream shredders (Heard and Richardson 1995). Whether this distribution pattern relates primarily to FPOM facilitation by upstream shredders or to physical partitioning of habitat along stream gradients remains to be seen. Habitat partitioning among taxa in this study indicates that physical habitat requirements, apart from those of food, are important in explaining longitudinal patterns along stream gradients. Multiple variables explained abundance patterns for taxa studied, supporting the idea that comprehensive approaches, where more than one environmental gradient is measured, are necessary before factors affecting species distribution and abundance patterns can be properly understood (Hall et. al. 1992).

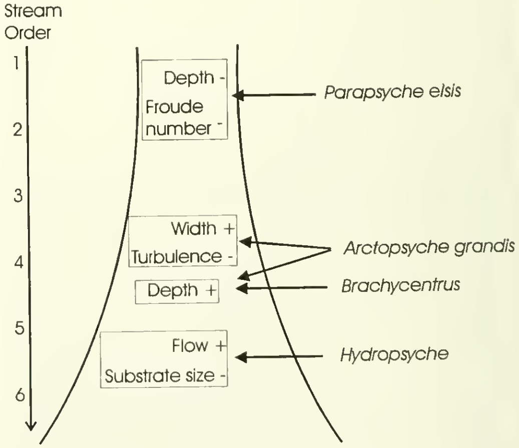

Fig. 2. Summary of major trends in species abundance among the 4 most common taxa studied and which environmental variables are most important in explaining those trends. Downstream gradient is depicted from small streams (1st–2nd order) through large systems (3rd–6th order). Positive and negative relationships are indicated by + and –, respectively.

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STEM GROWTH AND LONGEVITY DYNAMICS FOR *SALIX ARIZONICA* DORN

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ABSTRACT.—Diameter-age relationships of *Salix arizonica* (Arizona willow) stems were investigated for 5 populations on the Markagunt, Paunsaugunt, and Sevier plateaus in southern and central Utah. Of the 430 stems studied, none exceeded 26 mm in diameter at ground level (estimated age of 19 yr). Equations developed for predicting age from stem diameters consistently accounted for over 90% of the observed variation. Slopes of predictive equations were homogeneous across the 3 sites considered in detail. At 2 sites 46% and 38% of the stems exceeded 10 mm (~7 yr old) diameter at ground level. At a 3rd site, no stems survived to exceed that size. Stem-age profiles at specific sites may thus be useful for assessing the relative favorability of local environments for the species.

Key words: Arizona willow, Salix, *stem diameter, dendrochronology, southern Utah.*

The purpose of this study was to assess stem diameter–age relationships in *Salix arizonica* (Arizona willow), a species so rare that routine severance of stems for aging cannot be justified. Our objective was to develop a stem-age prediction model based on stem basal diameters. Ultimately, we desired to accurately estimate stem age at a broad range of ecological situations without sacrificing stems. We also evaluate the possibility of using stem-age profiles at an array of sites to determine their relative favorability for growth of *S. arizonica.*

DENDROCHRONOLOGY AS A TOOL

Growth rings of trees and shrubs have been used for many decades for aging stems and dating past climatic events (Douglas 1935, Glock 1937). Growth rings are also used to establish unique sequences of good and poor years that permit dating nonliving tree fragments used in prehistoric human structures (Schulman 1956, Fritts 1971, Stockton and Meko 1975, Harper 1979). Ring-width variations are often used to assess differences in the favorability of various environments for the growth of selected species (Ferguson and Humphrey 1959, Fritts 1962, Stockton and Fritts 1973, Fritts 1974). Although these studies have focused mainly on trees (Glock 1955, Argeter and Glock 1965), some have dealt with shrub species (Ferguson 1958, 1959, Ferguson and Humphrey 1959, Brotherson et al. 1984, 1987). Shrub studies have detailed the effects of variations in available moisture on plant growth in specific habitats or provided information for interpreting archaeological problems. Ring counts have also been used to predict stem diameter–age relationships in predictive models for interpreting site quality for various species or for clarification of successional patterns in vegetation that includes many woody species (Brotherson et al. 1984, 1987).

THE SPECIES AND ITS DISTRIBUTION

Salix arizonica is small. Rarely do stems exceed 1.0 m in height. The species occurs in such dense carpets of other species (both vascular and nonvascular) that reproduction via its tiny, wind-dispersed seeds appears to be uncommon. Accordingly, the species apparently persists at occupied sites primarily by vegetative reproduction. In the process, what appear to be large clones (as much as 10 m across) may develop.

Salix arizonica occurs in 2 disjunct locations in the Intermountain West. The species was first discovered on the White Mountains of east central Arizona by Carl-Eric Granfelt in 1969 (Galeano-Popp 1988). Robert Dorn (1975) used holotype specimens collected by Granfelt to describe the species in 1975. In November 1992, unaware that the species occurred in Utah, the U.S. Fish and Wildlife Service proposed *S. arizonica* for listing as endangered with designation of critical habitat (Atwood 1995). In June 1993 a previously misidentified herbarium specimen of S. *arizonica* was discovered; it had been collected on the "Sevier Forest" (now Dixie National Forest) in 1913. During June 1994, S. *arizonica* was discovered on the Markagunt Plateau near Brianhead resort area. Subsequent searching revealed a small population on the Paunsaugunt Plateau and 2 more farther north on the Sevier Plateau (Mead 1996). Following this "rediscovery" of S. *arizonica* in Utah, USDA Forest Service, USDI Fish and Wildlife Service, and USDI National Park Service officials cooperated in developing a conservation agreement and strategy that outlines the "actions, costs and skills needed to implement protective measures and research studies needed for the species" (Atwood 1995). As a result of the conservation agreement and strategy, which documents long-term plans for conservation of S. *arizonica*, the Fish and Wildlife Service withdrew their proposed rule to list the species as endangered (Arizona Willow Interagency Technical Team 1995).

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Although the species is locally abundant near Brianhead, its total range is small in both Arizona and Utah, and populations rarely include more than a few score plants. This rarity seems related to the plant's preference for an uncommon habitat: it grows preferentially on igneous soils in cold, wet sites. In addition, in the White Mountains, management has favored conifers that reduce flow in riparian systems, leading to poor drainage as waterways become peat-choked. Such environments become poorly aerated and less suitable habitat for S. *arizonica*. Heavy use by elk has also adversely affected the species in Arizona (Arizona Willow Interagency Technical Team 1995). This study has been confined to the Utah populations of *Salix arizonica* (Fig. 1), but we have attempted to sample the full range of conditions associated with the species in our study area.

METHODS AND STUDY AREAS

The diameter-age data for S. *arizonica* were collected from 3 populations: 2 on the Cedar City Ranger District and another on the Powell Ranger District, Dixie National Forest (Fig. 1). The Rainbow Meadows, Lowder Creek, and East Fork of the Sevier River populations were chosen because they represent environmentally intermediate (Lowder Creek) as well as extreme environmental conditions for S. *arizonica* in Utah. The Rainbow Meadows site occurs on acid soils at near maximal elevations for the species, while the East Fork of the Sevier River population occurs on alluvium derived from calcareous substrates at the lowest elevation known for the species.

Depth of peat layer was determined at each site by digging pits to expose soil profiles (Mead 1996). At Lowder Creek, Sheepherder Camp, and Sevenmile Creek, depth to water table was determined by opening a hole approximately 1 m deep with a 1.27-cm-diameter pointed rod, then inserting a 0.64-cm-diameter wooden dowel into the hole to measure depth to water. This measurement was taken at each plant sampled and an average value was computed for each site. Depth to water table at Rainbow Meadows was determined by measuring distance from soil surface to water table surface in a soil pit (Mead 1996). Depth to water table was determined at the East Fork site by measuring distance from the soil surface to the surface of water running in the creek. This measurement was taken at each S. *arizonica* clone; the mean distance is reported in Table 1. Depth of peat layer and depth to water table are variable among the study sites, with the Rainbow Meadows site having the highest water table and greatest peat depth (Table 1).

Two other populations of S. *arizonica* are considered in this report. Populations at Sheepherder Camp, Sevenmile Creek, and Lowder Creek have been sampled to establish stem-diameter profiles based on samples of many randomly chosen stems (154, 104, and 130 stems, respectively, sampled at the 3 foregoing sites). No stems were severed for aging at the Sheepherder or Sevenmile sites.

The Rainbow Meadows site is approximately 1.6 km south and slightly east of Brianhead Peak at approximately 3155 m elevation (37°40′N, 112°56′W). Soils are derived from tertiary volcanics with a histosol surface horizon (Mead 1996). The Lowder Creek population is approximately 4 km east and slightly south of Brianhead Peak (37°41′N, 112°48′W). Soil at this site is developed from tertiary volcanic material below an alluvium surface layer (Mead 1996). The East Fork population, approximately 48 km from the Lowder population (37°26′N, 112°21′W), is at the lowest elevation known for

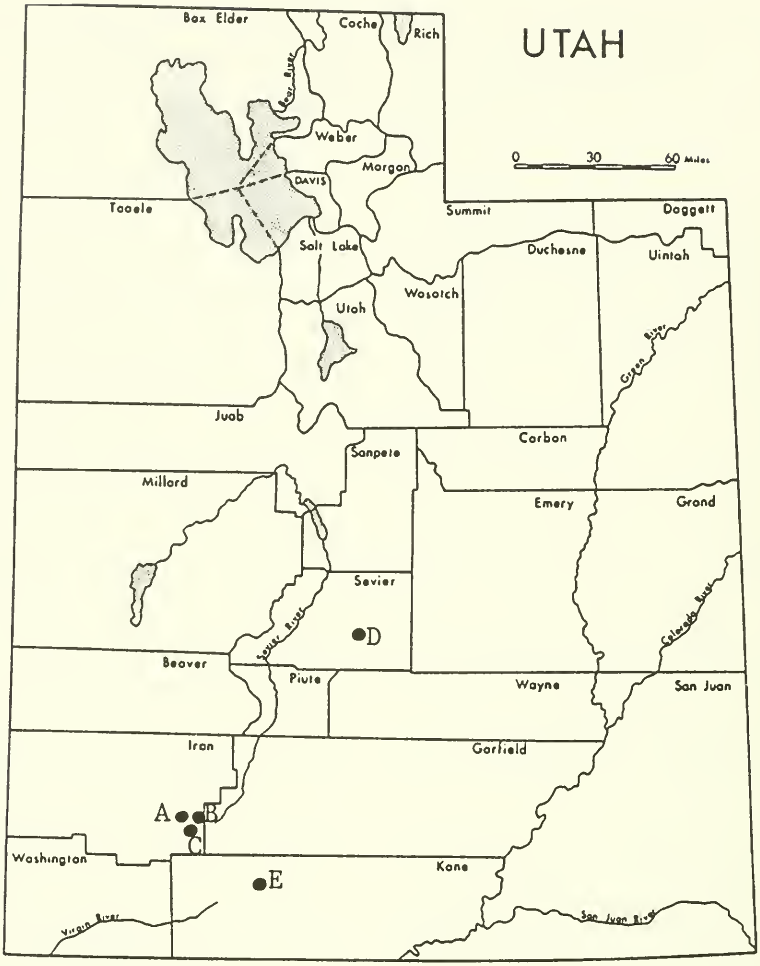
UTAH
0 30 60 Miles
Box Elder
Cache
Rich
Bear River
Weber
Morgan
DAVIS
Tooele
Summit
Daggett
Salt Lake
Duchesne
Uintah
Wasatch
Utah
Green River
Juab
Carbon
Sanpete
Millard
Emery
Grand
Sevier
D
Sevier River
Colorado River
Beaver
Piute
Wayne
San Juan
Iron
Garfield
A
B
C
Washington
Kane
E
Virgin River
San Juan River

Fig. 1. A, Rainbow Meadows; B, Lowder Creek; C, Sheepherder Camp; D, Sevenmile Creek; E, East Fork of the Sevier River.

this species in Utah. This population grows on alluvium from the Claron Limestone Formation with an organic surface horizon (Mead 1996).

Commonly associated plants at the sites sampled include *Salix planifolia, Polygonum bistortoides, Aconitum columbianum, Carex microptera, Geranium richardsonii, Geum macrophyllum,* and *Pedicularis groenlandica* (Mead 1996). As Mead (1996) has shown, the relative abundance of these species varies from site to site depending on such variables as soil temperature, depth to water table, and soil reaction.

Fifteen randomly chosen stems were sampled at each site at the Rainbow and Lowder locations. At each site 4 quadrants were established around randomly chosen points. The stem closest to the random point in each of 5 size-classes was collected in each of 3 quadrants (the right rear quadrant was not sampled). Stems were severed at ground level using wire cutters or a small hand saw. The diameter-classes sampled were 0–5 mm, 5.1–10 mm, 10.1–15 mm, 15.1–20 mm, and >20 mm at ground level. Thus, 3 stems per size-class were sampled at each site. Due to the low density of *S. arizonica* at the East Fork site, quadrants were not used. Stems were collected from all *S. arizonica* clones inside a livestock-grazing exclosure in the study area. No stems could be found at this site for the >20 mm size-class, so only 12 stems were sampled.

Stem samples were labeled, placed in individual bags, and taken to the lab. Stem bases

TABLE 1. Environmental conditions at 5 *Salix arizonica* sites. Water table was taken at all plants sampled wherever soil stoniness permitted insertion of the dowel to water depth. At East Fork water depth was based on only 16 points because only 16 plants exist at that site. The measure of variance around water table mean depth is standard error.

Site	Elevation (m)	Soil pH	Soil temp. @ 50-cm depth (°C)	Mean depth to water table (cm)	Peat depth (cm)
Rainbow	3155	5.15	8.3° (September)	5.1 ± NA	32
Lowder	3139	5.79	10° (August)	45.5 ± 1.81	0
Sheepherder	3130	5.72	6° (August)	44.4 ± 1.60	44
Sevenmile	2789	6.38	10° (August)	10.5 ± 1.12	0
East Fork	2536	7.61	16° (July)	46.5 ± 6.89	0

NA = not available.

TABLE 2. Regression equations relating stem diameter to age of *Salix arizonica* stems taken from 3 different sites. The regression equation for all sites combined is also shown. In the equation the independent variable, X, represents stem diameter (in mm). The symbol Y represents estimated age of any given stem.

Site	No. of stems	Equation	R^2	Significance level
Lowder	15	$Y = -0.42 + 0.82X$	.953	0.01
Rainbow	15	$Y = -0.28 + 0.78X$	.950	0.01
East Fork	12	$Y = -1.40 + 0.71X$	.910	0.01
All 3 sites combined	42	$Y = -0.99 + 0.81X$	.926	0.01

were sectioned diagonally and sanded with fine sandpaper; growth rings were counted twice (once by each of 2 observers) with the aid of a stereoscopic microscope (Brotherson et al. 1987). Diagonally cut surfaces permitted growth rings to be identified with greater confidence. Sanded surfaces sometimes had to be polished with immersion lens oil to enhance ring visibility. Each growth ring was assumed to represent 1 yr's growth. Linear regression was used to quantify stem diameter–age relationships.

RESULTS

S. arizonica stems from the 3 sites at which stems were cut and aged ranged in basal diameter from 2 to 26 mm and in age from 1 to 19 yr. Stem diameters (mm) were plotted against stem age (yr), and regression equations were generated (Table 2). Slopes for regression equations from the 3 sites were tested for similarity using methods described in Snedecor and Cochran (1967) and were found not to differ significantly ($P > 0.50$). Thus, data from all sites were pooled to produce a single equation ($Y = -0.99 + 0.81X$) for subsequent use in estimating age (Y) from diameter (X) (Fig 2).

As a further test of the validity of pooling data from all sites, we used the individual estimator equation developed for each site to predict age of willows collected from the other 2 sites (i.e., Rainbow equation used to test Lowder and East Fork samples, Lowder equation used to test Rainbow and East Fork samples, etc.). These analyses demonstrated that estimated ages for any equation–test site combination were always strongly correlated with actual age (R^2 always > .90). In these analyses no stems were found to differ from predicted age based on diameter by more than 3 yr, and most stems (>90%) differed by less than 2 yr (Fig. 1).

An application of the age-estimator equation is shown in Figure 3. As part of the yearly monitoring program, basal diameters of *S. arizonica* were taken for a large sample of stems at each of 3 sites: Sheepherder Camp, located approximately 8 km south of Brianhead Peak at 3130 m elevation (37°37′N, 112°56′W); Sevenmile Creek, 11 km north of Fish Lake in the Fishlake National Forest, Loa Ranger District at 2789 km elevation (38°39′N, 111°40′W); and Lowder Creek (described above). At each of these sites, the numbers of stems within each diameter-class were tabulated and are reported as percent of total stems in each size-class. The results (Fig. 3) demonstrate large differences in stem-diameter profiles among the 3 sites. At Sheepherder Camp over 4% of the stems are

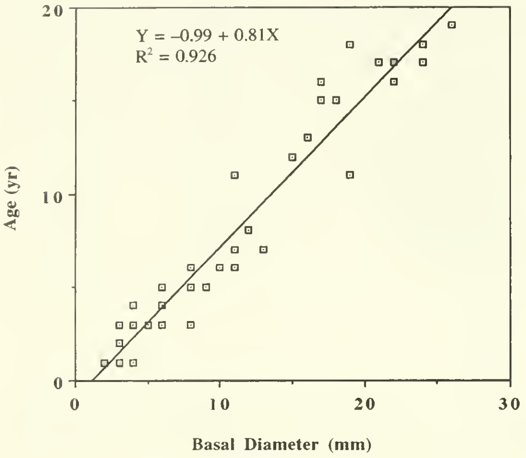

Fig. 2. Stem basal diameter–age relationships of S. *arizonica* on the Markagunt and Paunsaugunt plateaus of southern Utah.

larger than 20 mm diameter at ground level. However, less than 1% of the stems at Lowder Creek exceed that diameter, and at Sevenmile Creek no stems have survived to become 10 mm in diameter. These results suggest that Sheepherder Camp is a more favorable site for growth of the willow than either Lowder Creek or Sevenmile Creek. Alternatively, the results may indicate that willows are less severely browsed by ungulate grazers at Sheepherder Camp than at the other 2 sites. Since ungulate exclosures were not erected at these sites until fall 1994, data are currently too limited to distinguish between these alternatives.

DISCUSSION

The regression equation created from the pooled data of all 3 sites should be useful for predicting ages of S. *arizonica* from any known Utah location using only basal stem diameters. The equation should be useful for many projects in which stem age is desired but stems cannot be sacrificed. For example, the ability to estimate age of stems accurately from basal diameter may permit scientists studying the species to correlate stem ages and stem-age profiles with site conditions without destroying individual stems.

The results of this study demonstrate little variation in stem growth rates for S. *arizonica* over a wide range of elevations and parent materials (Table 1). That result suggests that the species occupies but a narrow range of habitat

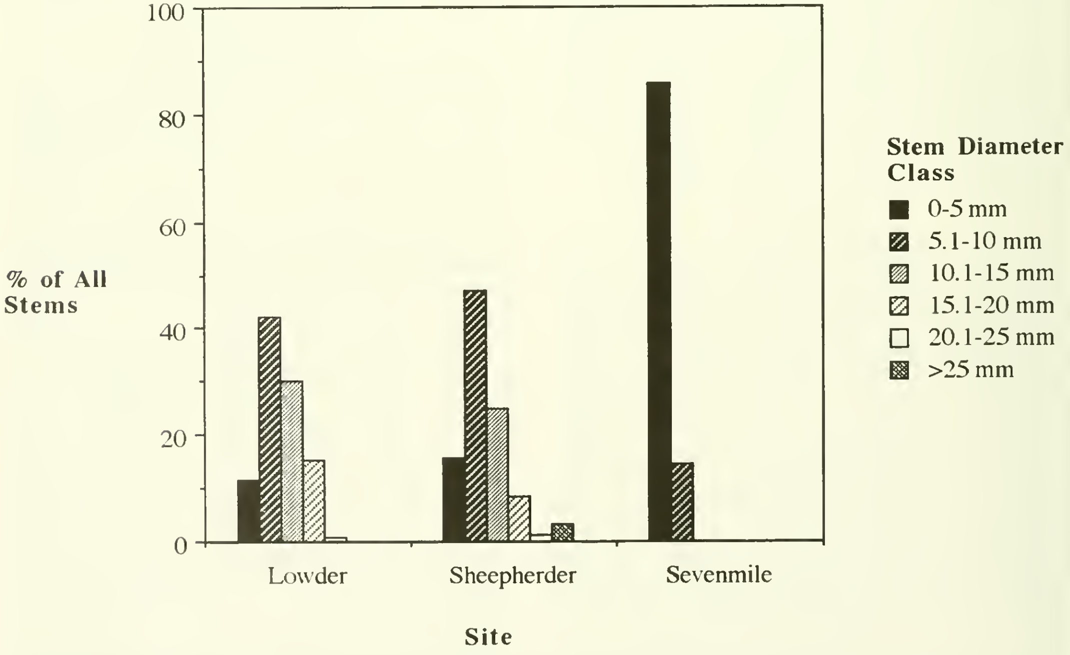

Fig. 3. Comparative stem diameter distributions for sites for which a large, random inventory of stem diameters was available.

situations within its overall geographic range. Occupied sites almost always appear to have been modified by biological processes that result in peat deposition and development of a rooting zone that is somewhat isolated from the unaltered geologic substrata at the site.

Stem-age profiles should permit managers to identify sites where performance (stem survival and/or reproduction by seed or rhizome) of the willow is above or below regional averages. Such data would help managers determine whether growth and reproduction of the species could be enhanced by reduction of use by browsers. To assist managers with such decisions, fenced areas that exclude domestic and wild ungulate browsers have been erected at Lowder Creek, Sheepherder Camp, and on the East Fork of the Sevier. An additional exclosure will be built at Sevenmile Creek in 1996.

The U.S. Forest Service intends to continue monitoring *Salix arizonica* populations throughout its range to learn about factors that influence growth, reproduction, and stem survival. Data from grazing exclosures will reveal the extent to which browsing controls stem size and longevity. The extent to which the abiotic environment limits stem growth and seed production can be more readily separated from the effects of browsing now that animal exclosures have been constructed.

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SOURCES OF VARIATION IN COUNTS OF MERISTIC FEATURES OF YELLOWSTONE CUTTHROAT TROUT (*ONCORHYNCHUS CLARKI BOUVIERI*)

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ABSTRACT.—We determined variability in counts of meristic features (pyloric caecae, vertebrae, pelvic fin rays, gillrakers, basibranchial teeth, scales above the lateral line, and scales in the lateral series) of Yellowstone cutthroat trout (*Oncorhynchus clarki bouvieri*) by 3 independent readers, by the same reader on 3 different occasions, and among fish from 12 sampling sites within a 650-km^2 watershed. Genetic purity of the cutthroat trout was determined by electrophoretic analysis. Significant differences in meristic counts were observed among 3 readers and among sampling sites, but not among 3 occasions by a single reader. Scale counts were within the reported range for Yellowstone cutthroat trout, but counts of other structures (pyloric caecae, gillrakers, vertebrae) were as similar to rainbow trout as to Yellowstone cutthroat trout. Meristic counts identified the fish as cutthroat trout; however, variation among readers and sampling sites, as well as within the species, limits their use when identifying genetically pure cutthroat trout or assessing possible integration with rainbow trout.

Key words: meristic counts, Yellowstone cutthroat trout, meristic variation, genetics, rainbow trout, conservation biology.

Hybridization of native cutthroat trout (*Oncorhynchus clarki*) with introduced rainbow trout (*O. mykiss*) has contributed to the decline of cutthroat trout in the western United States (Allendorf and Leary 1988, Gresswell 1988, Behnke 1992). An important initial step toward restoration or preservation of native cutthroat trout populations is reliable identification of genetically pure populations (Rinne 1985, Leary et al. 1989).

Meristic features, such as fin ray or vertebrae counts, have been used to identify hybridization among species of trout. The technique assumes that hybrids are intermediate to parental taxa and have increased morphological variance (Leary et al. 1985, 1991, Marnell et al. 1987). This assumption is not always valid and meristic comparisons can provide misleading taxonomic information (Leary et al. 1984, 1985, Currens et al. 1989). Environmental influences and observer error are 2 factors that can lead to variation in meristic counts for a species among sampling sites (Currens et al. 1989, Leary et al. 1991, Hubert and Alexander 1995). Even though more definitive biochemical methods have been developed (Leary et al. 1987, 1989, Nielsen 1995), biologists continue to use meristic features to assess genetic purity of cutthroat trout populations (Loudenslager and Gall 1980, Rinne 1985, Behnke 1992).

Protein electrophoresis is a reliable method of determining genetic status of trout populations (Marnell et al. 1987, Leary et al. 1989, Nielsen 1995). Electrophoresis provides data on allelic frequencies at genetic loci for different populations (Avise 1974). Hybridization can be determined when allele frequencies unusual for a particular species are found at several diagnostic loci that occur between taxa (Ayala and Powell 1972, Leary et al. 1989). For example, Yellowstone cutthroat trout (*O. c. bouvieri*) can be differentiated from rainbow trout using alleles at 10 diagnostic loci (R. Leary, University of Montana, personal communication).

If this procedure is valid, managers could save considerable time and money using meristic features instead of biochemical analysis to assess genetic purity of cutthroat trout. However, unless variation in meristic counts is minimal among readers or sampling sites, the usefulness of meristic features in adequately assessing genetic purity will be limited. The objectives of this study were to determine variability in counts of meristic features (1) among

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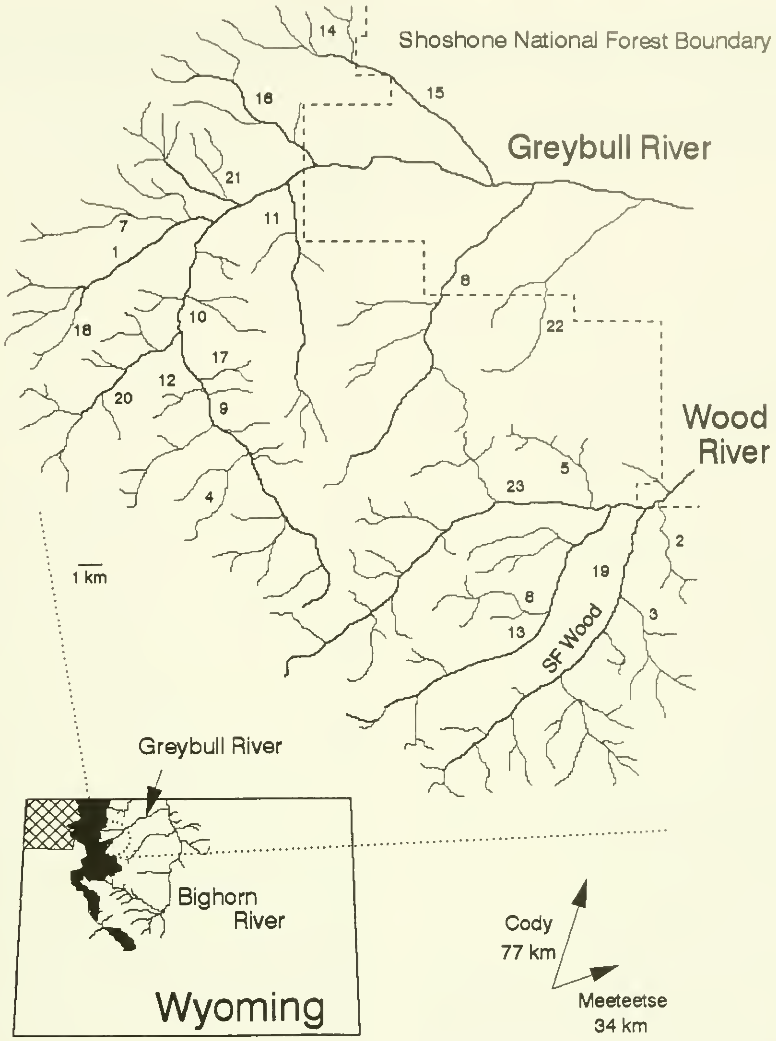
14
Shoshone National Forest Boundary
15
16
Greybull River
21
11
7
1
8
22
10
18
17
12
20
9
Wood River
23
5
4
1 km
2
19
6
3
13
SF Wood
Greybull River
Bighorn River
Wyoming
Cody
77 km
Meeteetse
34 km

Fig. 1. Map of Wyoming showing the location of the Greybull River drainage. Sites where cutthroat trout were sampled are numbered in reference to Table 1.

independent readers, (2) among counts by a single reader, and (3) among sampling sites within a moderate-sized watershed (650 km^2).

STUDY AREA

The Greybull River drains 2900 km^2 of the eastern Absaroka Mountain Range in northwestern Wyoming. The study area includes that portion of the Greybull River drainage within the Shoshone National Forest (Fig. 1). A total of 56 perennial tributaries (355 km of total stream length) occur in the 650-km^2 headwater drainage.

The Greybull River and its tributaries are torrential, high-elevation mountain streams with high channel slopes, unstable substrates, and large fluctuations in discharge from spring to late summer. Elevations of streams in the study area range from 2300 to 3050 m above mean sea level.

The Greybull River, within the historic range of Yellowstone cutthroat trout (Behnke 1992), is currently managed by the Wyoming Game and Fish Department as a sport fishery for native cutthroat trout and mountain whitefish (*Prosopium williamsoni*). Nonnative brook trout (*Salvelinus fontinalus*), finespotted cutthroat

TABLE 1. Streams containing cutthroat trout in the Greybull River drainage, number of fish collected, and sample sizes from each used for meristic counts and analysis. Genetic status indicated by pure Yellowstone cutthroat trout (P) or potential finespotted cutthroat trout hybridization (FSC). Number preceding the stream name corresponds to sites in Figure 1.

Stream		Number of fish collected	Allozyme analysis	Counted by all readers	Counted by single reader
1	Anderson	15	15 (P)	5	14
2	Brown	17		10	16
3	Chimney	16			15
4	Cow	16			11
5	Deer	16		4	16
6	Dundee	2			
7	Eleanor	19			3
8	Francs Fork				
9	Upper Greybull	15			7
10	Lower Greybull	20	20 (P)	1	20
11	Jack	21	19 (FSC)		10
12	Mabel	2		2	2
13	MF Wood	15	15 (FSC)		3
14	NF Pickett				
15	Picket	17	19 (P)		4
16	Piney				
17	Red	4		4	4
18	SF Anderson				
19	SF Wood	18	15 (FSC)	8	
20	Venus	16		9	10
21	Warhouse	18			14
22	W Timber				
23	Wood	21	20 (FSC)	7	18

trout, and rainbow trout have been stocked in the system.

METHODS

Twenty-three streams in the Greybull River drainage were sampled with battery backpack electroshockers from June to September 1994. Cutthroat trout were collected from 1 site (12–20 fish) on each of 18 streams. For analysis purposes the upper and lower Greybull River sites were considered separately (Table 1). Fish were collected from the midpoint of the length of each stream in which cutthroat trout were found. A sample of eye, liver, and muscle tissue was removed from each fish, wrapped in aluminum foil, and frozen within 1 h in liquid nitrogen. The remainder of each specimen was preserved in 75% ethyl alcohol. Tissue samples from each fish were individually identified.

Frozen tissue samples from 7 of the 18 streams were sent to the Wild Trout and Salmon Genetics Lab (WTSGL) at the University of Montana, Missoula, for genetic analysis. The 7 sites were selected to represent fish distribution in the drainage (Table 1, Fig. 1). Also, they were close to locations where finespotted cutthroat trout and rainbow trout had been previously introduced in the drainage (Wyoming Game and Fish Department records). Protein electrophoresis (Allendorf and Phelps 1980, Leary et al. 1984, Perkins et al. 1993) was performed to detect each specimen's genetic characteristics at 45 loci in muscle, liver, or eye tissue. Allele frequencies at 10 diagnostic loci (Table 2) were evaluated to determine hybridization with rainbow trout. Additionally, the presence of the AK-1*333 allele was evaluated to detect possible finespotted cutthroat trout hybridization.

Seven meristic features were counted on the preserved cutthroat trout: (1) basibranchial teeth, (2) anterior gillrakers (upper and lower limb of the first branchial arch), (3) pelvic fin rays, (4) scales in the lateral series, (5) scales above the lateral line, (6) pyloric caecae, and (7) vertebrae (Marnell et al. 1987, Behnke 1992). Three independent readers (all fisheries biologists with training in anatomy and taxonomy of salmonids) counted each meristic structure on the same 50 cutthroat trout (≥ 150 mm total length) chosen randomly from 9 of the 18

TABLE 2. Alleles at the 10 diagnostic loci that distinguish Yellowstone cutthroat trout and rainbow trout along with the tissue needed for each. The most common allele existing at each loci is listed first.

	Characteristic alleles		
Locus	YSC	RBT	Tissue
SAAT-1*	165	100,0	Liver
CK-A2*	84	100	Muscle
CK-C1*	38	100,150,38	Eye
mIDHP-1*	75	100	Muscle
sIDHP-1*	71	100,114,71,40	Liver
sMEP-1*	90,100	100	Muscle
sMEP-2*	110	100,75	Liver
PEPA-1*	101	100,115	Eye
PEPB*	135	100	Eye
PGM-1*	null	100,null	Muscle

streams (Table 1) 3 different times to assess repeatability and variation of counts within and among individual readers. One reader counted the 7 meristic features on 125 additional cutthroat trout to determine mean counts for each structure and allow comparison among the 12 sampling sites where ≥ 5 fish were counted (Table 1). The initial count from this reader's original 50 fish was also included in the analysis, leading to a sample of 175 cutthroat trout.

All counts were done on the right side of each cutthroat trout. Scales in the lateral series were counted 2 scale rows above the lateral line starting at the opercle opening and continuing to the insertion of the caudal fin, while scales above the lateral line were counted from the anterior of the dorsal fin on a vertical diagonal down to the lateral line. Vertebrae were counted during dissection of the fish. Pyloric caecae were enumerated by stretching the stomach and counting caeca ends. Meristic features were counted under a dissecting microscope using 30X magnification and reflected light. Readers practiced the protocol and compared results to resolve procedural differences before initiation of counts. All fish were counted at similar times by each reader with several different cutthroat trout counted between subsequent counts.

Three-way analysis of variance (ANOVA) was used to assess differences in counts of meristic features among (1) readers, (2) readings by individual readers, and (3) sampling sites. The sampling site effect was then controlled for and a 2-way ANOVA was used. One-way ANOVA was used to compare counts among readers and sampling sites. Tukey's multiple comparison test was used to make pairwise comparisons if significant differences were found. Statistical analyses were performed using SPSS/PC+ (SPSS Inc. 1991). Significance was determined at $P \leq 0.05$ for all tests.

RESULTS AND DISCUSSION

Cutthroat trout were present in all 23 study streams. Electrophoretic analysis of fish from 7 streams found no genes at diagnostic loci that identify rainbow trout (Table 2). Because genetic samples were collected from sites most likely to contain rainbow trout alleles (e.g., streams stocked with rainbow trout), we considered all trout in the drainage to be pure cutthroat trout.

The AK-1*333 allele is common among finespotted cutthroat trout in the Snake River drainage and was detected in 4 of the 7 samples (Table 1). This allele, while not unique to finespotted cutthroat trout, is rare in Yellowstone cutthroat trout populations outside the Snake River drainage; its presence indicates possible integration with finespotted cutthroat trout. An ANOVA showed no consistent difference in counts for any of the 7 meristic features between fish from sites potentially hybridized with finespotted cutthroat trout and those considered pure Yellowstone cutthroat trout. Additionally, Behnke (1992) stated that meristic counts of finespotted and Yellowstone cutthroat trout are indistinguishable, and there is considerable debate as to whether finespotted cutthroat trout are a formal subspecies. Therefore, we did not differentiate between finespotted and Yellowstone cutthroat trout in our analysis.

No significant differences among counts by the same reader for any meristic feature were observed. All 3 readers had high agreement among multiple counts for each structure (Table 3).

Significant differences in mean counts among different readers were observed for all structures except gillrakers (Tables 4, 5). All 3 readers had significantly different mean counts of pyloric caecae, pelvic fin rays, and scales above the lateral line, while at least 1 reader was significantly different from the other 2 readers in mean counts of vertebrae, basibranchial teeth, and scales in the lateral series. Hubert and Alexander (1995) also found poor agreement

TABLE 3. Significance values for differences in mean meristic counts among 3 readers (RDR), 3 readings by individual readers (RUN), and sampling site (SITE).

	Main effects			Interactions			
Structure	RDR	RUN	SITE	RDR×RUN	RDR×SITE	RUN×SITE	RDR×RUN×SITE
Pyloric caecae	0.000	0.903	0.000	1.000	0.000	1.000	1.000
Vertebrae	0.000	0.819	0.061	0.757	0.047	0.997	1.000
Pelvic fin rays	0.000	0.996	0.012	0.794	0.000	1.000	1.000
Gillrakers	0.765	0.356	0.244	0.352	0.045	0.098	0.051
Basibranchial teeth	0.448	0.945	0.000	0.952	0.323	1.000	1.000
Scales in lateral series	0.000	0.939	0.000	0.989	0.000	1.000	1.000
Scales above lateral line	0.000	0.986	0.000	1.000	0.000	1.000	1.000

TABLE 4. Significance values for the difference in mean meristic counts among 3 readers (READER) and among 3 readings by individual readers (RUN) at 5 sampling sites.

		Main effects		
Structure	Site	READER	RUN	Interaction
Pyloric caecae	Anderson	0.083	0.998	1.000
	Brown	0.000	0.993	0.808
	SF Wood	0.108	0.860	1.000
	Venus	0.227	0.932	0.972
	Wood	0.000	0.999	0.998
Vertebrae	Anderson	0.019	0.812	0.984
	Brown	0.000	0.618	0.561
	SF Wood	0.153	0.887	0.918
	Venus	0.016	0.886	0.969
	Wood	0.226	0.849	0.969
Pelvic fin rays	Anderson	0.000	0.802	0.924
	Brown	0.005	0.628	0.882
	SF Wood	0.000	0.880	0.924
	Venus	0.003	0.621	0.435
	Wood	0.000	1.000	1.000
Gillrakers	Anderson	0.596	1.000	1.000
	Brown	0.737	0.815	0.992
	SF Wood	0.001	0.871	0.492
	Venus	0.400	0.981	0.881
	Wood	0.055	0.938	0.880
Basibranchial teeth	Anderson	0.728	0.878	0.995
	Brown	0.000	0.683	0.902
	SF Wood	0.142	0.975	0.907
	Venus	0.064	0.889	0.990
	Wood	0.090	0.907	0.886
Scales in lateral series	Anderson	0.001	0.951	0.932
	Brown	0.000	0.860	0.818
	SF Wood	0.000	0.431	0.535
	Venus	0.000	0.879	0.905
	Wood	0.000	0.975	0.999
Scales above lateral line	Anderson	0.000	0.886	0.973
	Brown	0.000	0.888	0.843
	SF Wood	0.000	0.712	0.815
	Venus	0.000	0.885	0.885
	Wood	0.000	0.644	0.694

TABLE 5. Variation in mean meristic counts and standard deviations (in parentheses) of 3 readers. Means not significantly different indicated by bold (Tukey's $P \leq 0.05$).

	Reader			
Structure	1	2	3	*P*
Pyloric caecae	32.7 (6.3)	36.9 (9.5)	41.0 (11.7)	<0.0001
Vertebrae	60.5 (1.6)	**59.5 (2.0)**	**59.3 (1.2)**	<0.0001
Pelvic fin rays	9.0 (0.4)	8.8 (0.4)	9.4 (0.6)	<0.0001
Gillrakers	**18.9 (1.6)**	**18.8 (1.3)**	**19.3 (10.8)**	0.83
Basibranchial teeth	**13.7 (4.2)**	15.3 (4.3)	**14.2 (4.2)**	0.003
Scales in lateral series	178.0 (14)	**187.5 (14)**	**187.4 (13)**	<0.0001
Scales above lateral line	44 (4.2)	56.4 (5.2)	42.5 (3.6)	<0.0001

TABLE 6. Mean meristic counts and standard deviations (in parentheses) for 175 fish by 1 reader with ranges among the 12 sample sites with ≥5 fish counted. A probability (*P*) of ≤0.05 indicates significant differences among sites.

Structure	Grand mean (*s*)	Range in means among sites	*P*
Pyloric caecae	42.29 (10.89)	29.9–51.4	<0.0001
Vertebrae	58.57 (1.39)	57.9–60.6	0.0002
Pelvic fin rays	9.23 (0.86)	9.0–9.9	0.0001
Gillrakers	18.80 (2.08)	17.8–19.9	0.0018
Basibranchial teeth	13.96 (5.45)	11.4–21.8	0.0025
Scales in lateral series	182.70 (14.77)	175.5–207.3	<0.0001
Scales above lateral line	40.39 (3.51)	37.1–45.5	0.0001

among readers when counting meristic features of rainbow trout.

Significant differences were observed in counts of meristic features among fish from 12 streams (Tables 3, 6). Meristic features may be environmentally controlled within specific areas or drainages (Barlow 1961, Rinne 1985, Currens et al. 1989), but environmental variables measured at each sampling site (elevation, gradient, and stream size) were not correlated with meristic counts in the Greybull River drainage (Kruse 1995).

Researchers have used meristic counts with varied success to identify subspecies of cutthroat trout (Loudenslager and Kitchen 1979, Loudenslager and Gall 1980, Marnell et al. 1987). Recent research has shown that meristic comparisons can provide potentially misleading information (Busack and Gall 1981, Leary et al. 1984, 1985) because meristic characteristics are often specific to localized populations (Behnke 1992) and are strongly influenced by genetic variation (Leary et al. 1991).

Behnke (1992) described typical meristic counts for Yellowstone cutthroat trout and rainbow trout (Table 7). Mean counts of meristic features of cutthroat trout from the Greybull River drainage (Tables 5, 6) were within ranges for Yellowstone cutthroat trout (Table 7); however, mean counts of pyloric caecae, vertebrae, and gillrakers were also within typical ranges for rainbow trout. Variation and similarity in counts of meristic features of Yellowstone cutthroat trout and rainbow trout make it difficult to determine species or hybrids using meristic counts alone. Only the presence of basibranchial teeth provided a distinction between the 2 species.

Variations among readers, and among sampling sites in a small geographic area, along with relatively wide ranges in counts for Yellowstone cutthroat trout and rainbow trout, make it difficult to differentiate these 2 species with certainty using commonly assessed meristic features (Table 7). Furthermore, it is unlikely that Yellowstone cutthroat trout × rainbow trout hybrids can be identified due to the extensive variation in counts.

TABLE 7. Ranges of meristic counts among species (YSC = Yellowstone cutthroat trout and RBT = rainbow trout), readers, and sampling sites.

	YSC[a]		RBT[a]			
Variable	Typical	Overall	Typical	Overall	Variation among readers[b]	Variation among sampling sites[c]
Pyloric caecae	35-43	25-50	37-55	30-70	33-41 (36.9)	30-51
Vertebrae	61-62	60-63	62-64	61-66	59-61 (59.8)	58-61
Pelvic fin rays	9	9-10	not reported		9 (9.0)	9-10
Gillrakers	19-20	17-23	19-21	17-24	18-21 (19.0)	18-20
Basibranchial teeth		present		present	14-16 (14.4)	11-22
Scales in lateral series	165-180	150-200	125-150	120-160	179-188 (184)	176-207
Scales above lateral line	45-50	40-55	30-32	26-35	42-57 (47.6)	37-46

[a] From Behnke (1992)

[b] Ranges are from the 9 readings taken for each structure with means in parentheses (3 readings by 3 readers).

[c] Ranges are from means for the 12 sampling sites that had ≥ 5 cutthroat trout (≥ 150 mm total length) counted (Table 6).

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STUDIES ON NEARCTIC *NEGASTRIUS* (COLEOPTERA: ELATERIDAE)

Samuel A. Wells[1]

Abstract.—New species descriptions of *Negastrius rupicola* from California, Oregon, Washington, and British Columbia; *N. stibicki* from California, Montana, and British Columbia; *N. solox* from Arizona and New Mexico; and *N. atrosus* from Ontario and Quebec are given. *Negastrius colon* is returned to species status, and a neotype is designated for *N. choris*. *Fleutiauxellus extricatus* is a new combination. A key is provided to Nearctic species of *Negastrius*.

Key words: Negastrius, *Elateridae, holotype, paratype, neotype.*

History

Negastrius was established in the family Elateridae by Thomson (1859) to distinguish those species of *Cryptohypnus* Eschscholtz having arcuate prosternal sutures from species with straight or double sutures. Candeze (1860) did not use Thomson's assignments and placed all *Negastrius* species in *Cryptohypnus*. Horn's (1891) monograph of the species of *Cryptohypnus* of Boreal America rejected the name *Negastrius* and included all North American forms into 9 groups within the genus *Cryptohypnus*. Horn's *choris* group included *N. delumbis* (Horn), *N. choris* (Say), *N. exiguus* (Randall), and *N. ornatus* (LeConte), which were equivalent to Thomson's *Negastrius*. Schwarz (1906) included *Negastrius* and *Cryptohypnus* with the genus *Hypnoidus* Stephens in the tribe Hypnoidini. Leng (1920) also placed all species, except *N. exiguus*, in the genus *Cryptohypnus*. Using mesosternal characters, Nakane and Kishii (1956) made the distinction between the subfamilies Negastriinae and Hypolithinae (which they synonymized under the Cteniceriinae). Arnett (1963) recognized only the genera *Negastrius* and *Oedostethus* LeConte in the Negastriinae from North America. Stibick (1971) recognized or established *Neohypdonus* Stibick, *Migiwa* Kishii, *Oedostethus*, *Fleutiauxellus* Mequignon, *Negastrius*, *Zorochrus* Thomson, and *Paradonus* Stibick from North America. He restricted *Negastrius* to those species with coarse pronota, single prosternal sutures, and species with the 2nd and 3rd antennal segments equivalent in length. Later, Kishii (1976) erected *Microhypnus*, to which Stibick (1991) assigned the single North American species of *M. striatulus* (LeConte).

Discussion of Characters

With the exception of the Cardiophorinae, the subfamily Negastriinae is distinguished from other subfamilies of Elateridae by having the meso- and metasterna adjacent and separating the mesocoxal cavity from the mesepimeron and mesepisternum. The Negastriinae is distinguished from the Cardiophorinae by possession of a pointed prosternal process, which is shortened and truncated in the Cardiophorinae. Within the Negastriinae, *Negastrius* is apparently most closely related to the genus *Microhypnus*, both genera having a strigate and/or rugose pronotum. Following Stibick's (1971) presumed natural affinities, the sister group of *Negastrius* could be any of the North American genera, except *Paradonus*, which is more closely related to the Old World species of *Thurana* Stibick and *Optitarynus* Stibick, both of which are without externally visible elytral striae. *Zorochrus* is distinguished from *Negastrius* by the double prosternal sutures and/or by the arcuately extended pronotum that projects over the head. In addition, the pronotum in *Zorochrus* is more coarsely granulate on the anterior half. *Fleutiauxellus* differs from the other genera of Negastriinae by having the 3rd antennal segment nearly twice as long as the 2nd. The genus *Neohypdonus* is separated from *Negastrius* by a smooth to slightly punctate pronotum that is often shiny (Wells 1991). *Oedostethus* is distinguished from *Negastrius* by having a flange on the tarsal claws.

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Horn's (1891) key to *Negastrius* (sensu stricto) used leg and antennal coloration, pronotal carinae, and lateral and dorsal profiles of individuals to separate the 4 North American species known to him (*N. choris*, *N. delumbis*, *N. exiguus*, and *N. ornatus*). The strongly arched profile and the short submarginal pronotal carinae of *N. delumbis* are characters useful only in distinguishing that species. Horn's other characters are too variable to be useful in distinguishing species. The most valuable characters in comparing species and species groups include the shape of the scutellum and the relief of the anterior portion of the interstriae. These characters readily distinguish all North American species except *N. solox*, *N. ornatus*, and *N. colon*. These species are separated by the substrigose ridges on the prosternum and by the curvature of the posterior margin of the prosternum.

Both male and female genital characters have been used by Stibick (1991) to separate species. Slight differences do exist in the length and position of the setae on the parameres and in the thickness of the base of the aedeagus; however, these differences are as pronounced intraspecifically as they are interspecifically. On average, over 20 terminalia (per sex) were dissected per species in this study, except *N. solox* for which only 2 specimens were available. None of the species contained consistent patterns that would be of taxonomic use, except *N. nadezhdae*, which has a slightly angled tip of the aedeagus (Fig. 17).

CLASSIFICATION

Negastrius Thomson

Negastrius Thomson, 1859:106. Type-species: *Elater pulchellus* Linnaeus, 1758, original designation.

DIAGNOSIS.—The genus *Negastrius* in North America is distinguished from other Negastriinae by the curved and simple prosternal sutures; by the rugose or granulose pronotum; and by a row of parallel setae extending from the posterior margin of the 4th abdominal sternite onto abdominal sternite 5.

DESCRIPTION.—Length 1.8–5.7 mm, width/length ratio 0.3–0.4; color golden brown to black and normally with various arrangements of pale cuticular color patterns on the elytra. These color patterns include yellow or black maculae on the humeral angles of the elytra. Pale subapical maculae are also present on some specimens of *N. colon*, *N. atrosus*, and *N. ornatus*.

Head rugose to granulose; frontal carina transverse, evenly arcuate and margined between eyes, divided into 2 carinae immediately anterior to eyes; antennae short, never reaching posterior margin of pronotum; antennal segments 1–3 cylindrical, scape subequal in length to segments 2 and 3 combined, remaining segments slightly serrate; decumbent setae of antennae pale yellow to white, segments 3–11 each with 4–8 evenly distributed erect setae in addition to normal decumbent setae.

Pronotum rugose to granulose with carina of hind angle 0.2–0.8 times length of pronotum; pronotum with smooth median line from anterior margin to or near posterior margin, slightly convex to ridged; prosternal lobe extending over mouthparts; prosternal sutures single and slightly arcuate; prosternum more heavily and closely punctate than propleura; tarsi with each tarsomere progressively smaller than previous segment, except segment 5 which is subequal in length to segment 1, claws simple; scutellum punctate, gradually widening anteriorly.

Elytra elliptically narrowed posteriorly; posterior margin of abdominal sternite 4 with an even row of white to gold erect setae extending over anterior margin of abdominal sternite 5, setae more closely aligned and erect than other sternal setae.

Male genitalia with median lobe pointed and narrowed, gradually widening basally, 1.3 times longer than lateral lobes; lateral lobes straight on inner side, convex on outer apical third with 2 subapical setae. Female with bursa copulatrix membranous containing 1 anterior and 1 posterior lobe.

BIOLOGY.—North American species of *Negastrius* have been reported only in association with riparian habitats. *Negastrius delumbis* is the only species associated with coastal waters. It lives along the Atlantic seaboard north of Chesapeake Bay and south of Newfoundland. Most other species inhabit the sandy/rocky margin of streams and rivers. Adults are generally collected during the spring (except for some early records of *N. ornatus*) through early summer.

Key to the Species of North American *Negastrius*

1. Bases of elytral interstriae 2–5 strongly raised, forming a 90-degree angle in profile (Fig. 2); scutellum more strongly convex, anterior margin always emarginate (see Fig. 6) 2

— Base of elytral interstriae not or only slightly raised (Fig. 1); anterior margin of scutellum either emarginate (see Fig. 6) or medially extended (see Fig. 8) 4

2(1). Profile of elytra strongly arched on basal half; bases of interstriae 3 and 4 strongly elevated, each usually armed by a small tubercle; elytra golden brown to brown; pronotal carina 0.2–0.4 times length of pronotum (Fig. 4); length 2.7–5.2 mm; northeastern U.S. and SE Canada along coast and adjacent islands (Fig. 15) . . . . *delumbis* (Horn)

— Profile of elytra rather weakly arched on basal half; bases of interstriae 3 and 4 weakly elevated, lacking tubercles; black with pale maculations; pronotal carina 0.3–0.8 times length of pronotum 3

3(2). Pronotum longitudinally strigose, punctures distinct, rarely confluent; pronotal carina 0.3–0.6 times length of pronotum (Fig. 11); length 2.3–3.2 mm; northeastern U.S. and SE Canada west to North Dakota (Fig. 15) . . . . *nadezhadae* Dolin

— Pronotal strigosity obscure, punctures obsolete, ridges broken into rather coarse subconfluent tubercles; pronotal carina 0.6–0.8 times length of pronotum (Fig. 10); length 2.8–4.9 mm; California, Montana, and British Columbia (Fig. 14) . . . . *stibicki*, n. sp.

4(1). Anterior half of scutellum weakly convex, anterior border emarginate (Figs. 6, 9) 5

— Anterior half of scutellum medially elevated, anterior margin medially extended (Figs. 5, 8) . . 9

5(4). Anterior third of prosternum with 2 transverse impressions, area between margin and posterior impression with rugosities no different from rest of prosternum 6

— Anterior third of prosternum with 2 transverse impressions, area between margin and posterior impression with a series of conspicuous rugosities (Fig. 3) 8

6(5). Base of elytral interstria 3 elevated; prosternum convex on outer angle, equal to 0.17 length of basal margin; length 1.8–3.4 mm; northern California, Oregon, Washington, and British Columbia (Fig. 13) . . . . *rupicola*, n. sp.

— Base of elytral interstriae subequal in elevation; basal margin of prosternum convex on outer 0.12 or less 7

7(6). Pronotum distinctly strigose, ridges narrow and long; anterior margin of scutellum only slightly emarginate, almost straight (Fig. 6); 12–16 setae on outer angle of metatibia; length 2.6–3.6 mm; northeastern U.S. west to Iowa, south to North Carolina (Fig. 12) . . . . *exiguus* (Randall)

— Pronotum obscurely strigose, ridges short; anterior margin of scutellum strongly emarginate (Fig. 9); 16–27 setae on outer angle of metatibia; length 2.8–5.7 mm; western United States east to Colorado (Fig. 12) . . . . *colon* (Horn)

8(5). Pronotum with 2 shiny usually impunctate areas near middle of disc; elytra black with pale markings; length 2.9–5.4 mm; southern California (Fig. 14) . . . . *ornatus* (LeConte)

— Prosternum without shiny or impunctate areas on disc; elytra brown without pale markings; length 3.5 mm; Arizona and New Mexico (Fig. 13) . . . . *solox*, n. sp.

9(4). Carina of lateral margin of pronotum obsolete on anterior 0.25 (Fig. 7); pronotum longitudinally strigose with punctures in grooves anteriorly and laterally; mesosternum with a protruding knob on each side of mesosternal fossa; length 2.8–5.5 mm; eastern U.S. west to Nebraska (Fig. 13) . . . . *choris* (Say)

— Carina of lateral margin of pronotum extending to anterior margin; pronotal strigae fine and obscure, grooves impunctate; mesosternum without protruding knobs 10

10(9). Color brown with light bands or other patterns on elytra; scutellum more strongly pointed anteriorly (Fig. 5); length 2.5–3.9 mm; eastern U.S. and Canada west to North Dakota and Alberta (Fig. 14) . . . . *arnetti* Stibick

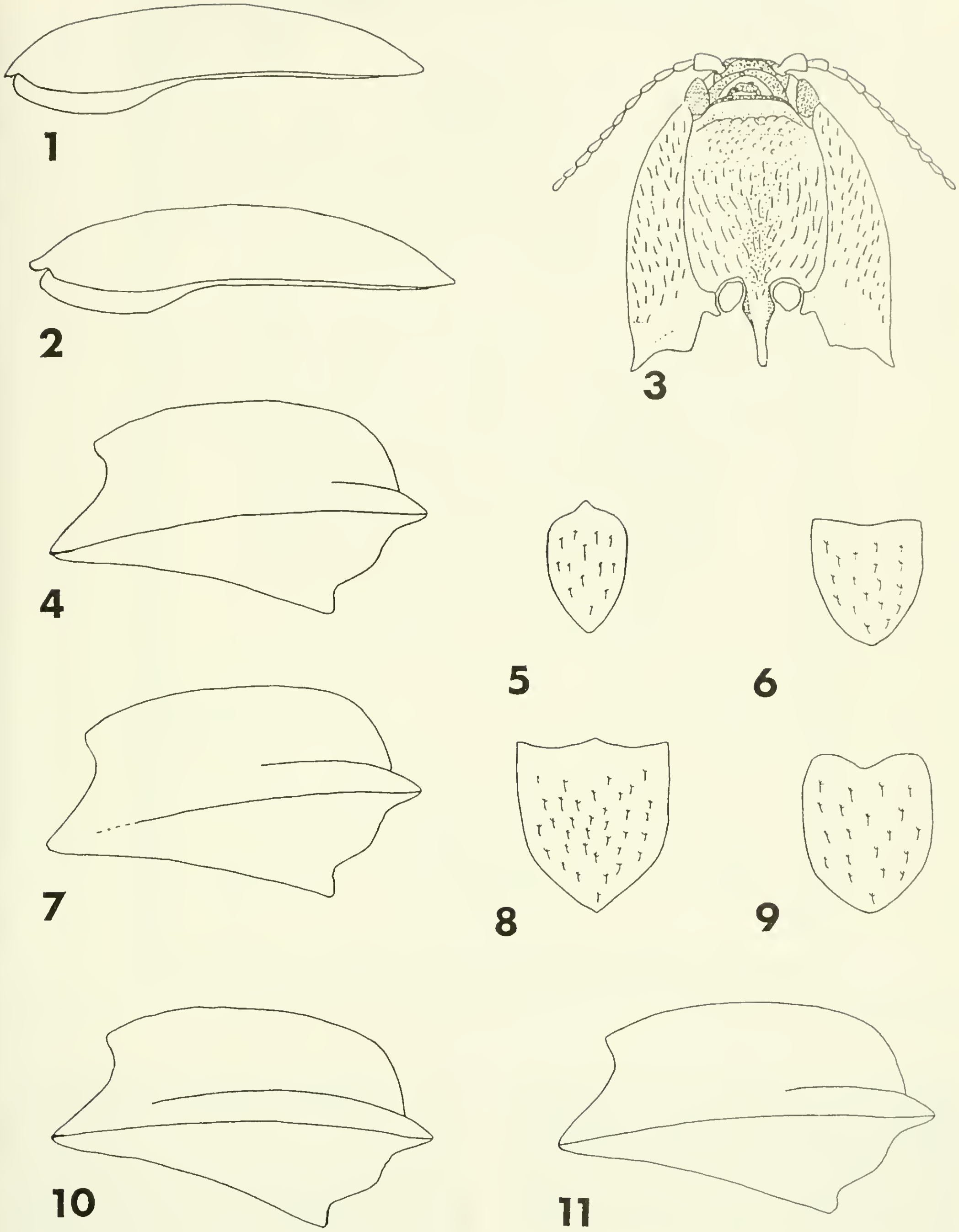
— Color black with 0, 2, or 4 pale elytral maculations; scutellum only slightly pointed anteriorly (Fig. 8); length 2.6–4.8 mm; Ontario and Quebec (Fig. 12) . . . . *atrosus*, n.sp.

Negastrius colon (Horn), new combination

(Figs. 9, 12)

Cryptohypnus colon Horn 1871:305.
Cryptohypnus ornatus colon; Horn 1891:17.
Cryptohypnus ornatus moerens Horn 1891:17. New synonym.
Hypnoidus ornatus colon; Leng 1920: 171, Schenkling 1925: 213.
Negastrius ornatulus Lane 1971: 19.

Horn's (1891) concept of *N. ornatus* included both the typical form with a pale band on the elytral disc, *N. colon* specimens with a similar band as in *N. ornatus*, and those specimens with 2 pale maculations on the posterior third of the elytra. He did not note the rugosities on the prosternal lobe. Horn's subspecies *N. ornatus moerens* represents completely black specimens of otherwise typical *N. colon*. Apparently, he did not see material with 2, 4, or 6 maculations on the elytral disc. In several areas, specimens with all color patterns and sizes occur together. In the vicinity of Lake Tahoe, California and Nevada, there is a form with the pale band on the elytra as well as golden brown



Figs. 1–11. *Negastrius* species: 1, *N. ornatus*, elytral profile; 2, *N. stibicki*, elytral profile; 3, *N. ornatus*, head and pronotum; 4, *N. delumbis*, pronotal profile; 5, *N. arnetti*, scutellum; 6, *N. exiguus*, scutellum; 7, *N. choris*, pronotal profile; 8, *N. atrosus*, scutellum; 9, *N. colon*, scutellum; 10, *N. stibicki*, pronotal profile; 11, *N. nadezhadae*, pronotal profile.

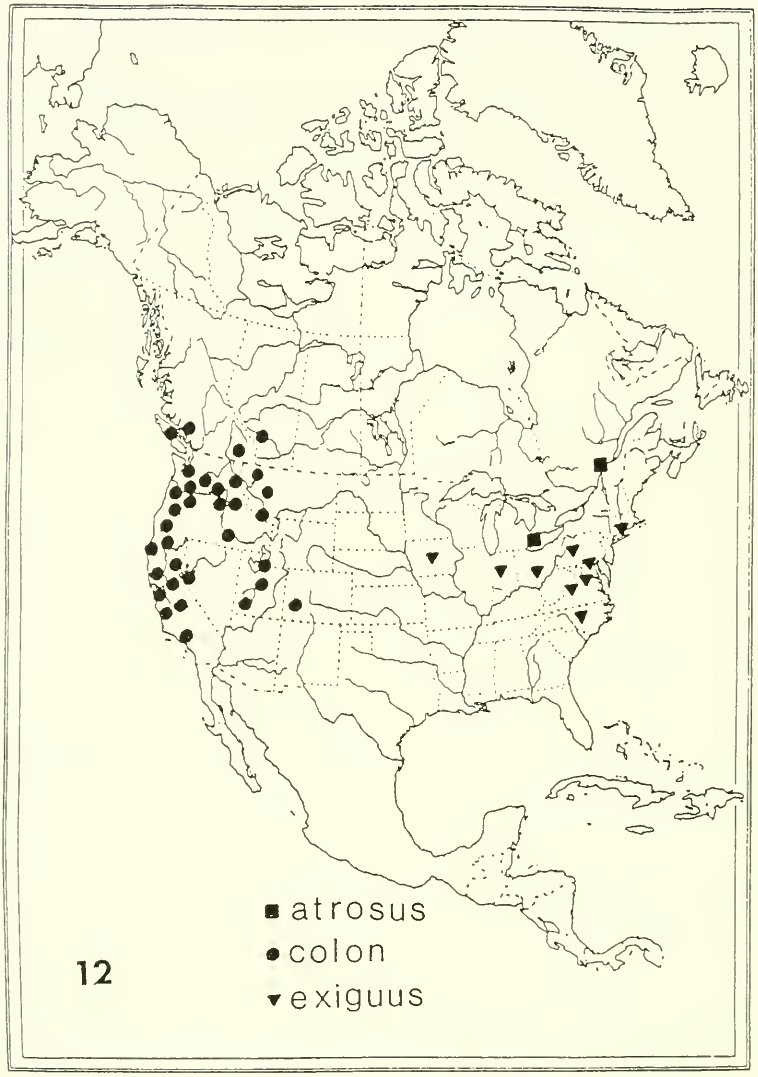


Fig. 12. Distribution of *Negastrius atrosus*, *N. colon*, and *N. exiguus*.

setae on the head and pronotum. This appears to be the only form in the area. There are a few specimens of this form from Seattle, Washington, along the Lostine River in Oregon, and in Parma, Idaho. The specimens from Utah and Colorado all have 4 pale maculations; this is the common form throughout the range of the species.

Negastrius colon is a common species in the western United States along the banks of small streams and larger waterways that have substantial riparian debris and ground cobbles. One population in Sanpete County, Utah, inhabits a small stream that is dry more than half the year.

Negastrius solox, new species

(Fig. 13)

DIAGNOSIS.—This species and *N. ornatus* are distinguished from other North American species of *Negastrius* by possessing strongly elevated rugosities on the prosternal lobe; it is distinguished from *N. ornatus* by the absence of pale maculations on the elytra.

DESCRIPTION.—Length 3.5 mm, width/length ratio 0.4; color brunneus, without maculations on elytra; profile elongate.

Head and pronotum granulose with a few granules forming short rugosities; median line of pronotum ridged; submarginal pronotal carina

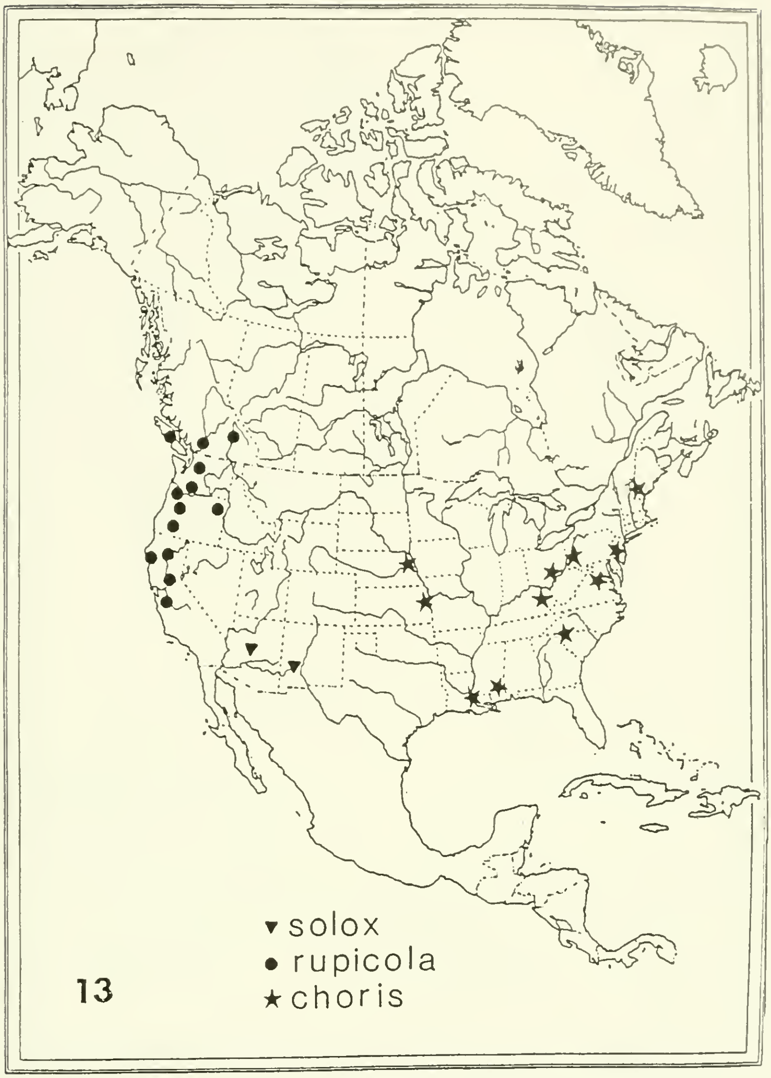


Fig. 13. Distribution of *Negastrius solox*, *N. rupicola*, and *N. choris*.

0.5 times length of pronotum; rugosities on the lobe of the prosternum elevated into ridges; posterior margin of prosternum evenly convex on lateral fourth; anterior margin of scutellum strongly emarginate; interstriae of elytral disc without punctures in center; lateral margin of mesosternal fossa evenly concave, without projecting knobs; outer angle of metatibia with 17 setae aligned along entire length.

HOLOTYPE.—Male, NEW MEXICO: Gila River, 19-VI-1901. Deposited in the Field Museum of Natural History, Chicago. Paratype (1) collected from ARIZONA: Yavapai Co., Prescott.

ETYMOLOGY.—The name *solox* is a Latin adjective meaning coarse or rough and refers to the strongly ridged rugosities on the prosternal lobe.

DISCUSSION.—This species is known from 2 specimens. The paratype from Arizona is in the USNM.

Negastrius nadezhadae Dolin

(Figs. 11, 15, 17)

Negastrius nadezhadae Dolin 1971:362.

This is the first report of this species for North America. Specimens examined were compared to 2 paratypes in the USNM. This small species occurs under stones along the banks of rivers in the eastern Tien Shan of central Asia.

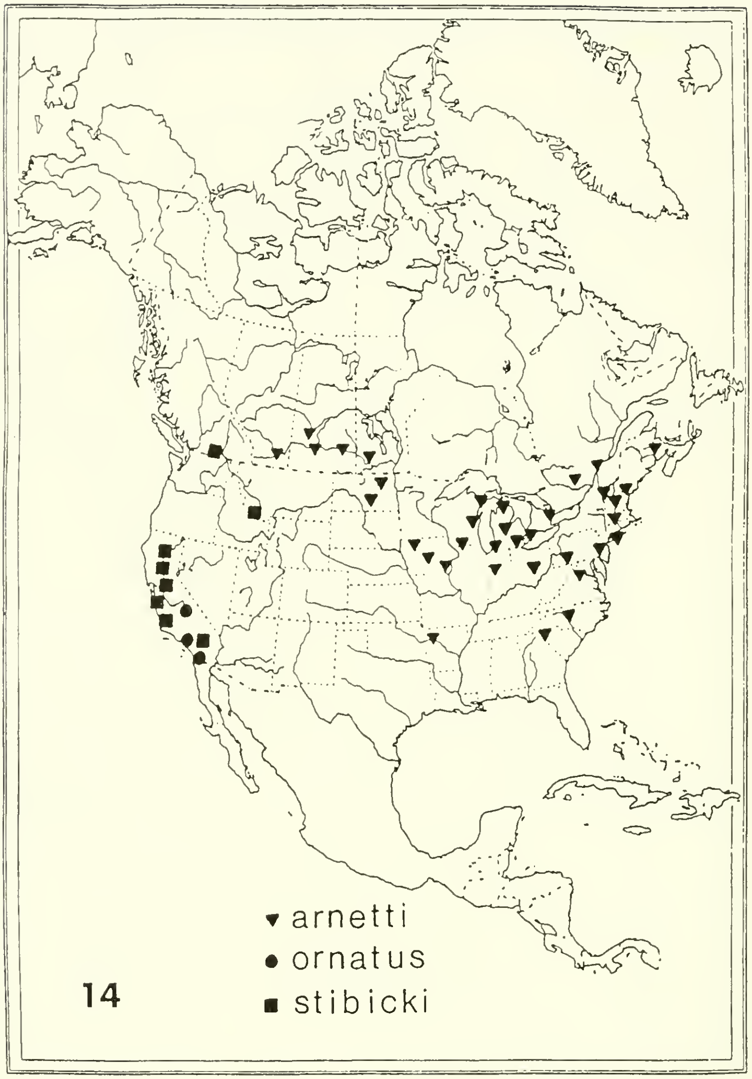


Fig. 14. Distribution of *Negastrius arnetti*, *N. ornatus*, and *N. stibicki*.

Four North American specimens were collected under lawn grass and by sweeping grass in Massachusetts and New Hampshire.

Negastrius stibicki, new species

(Figs. 2, 10, 14, 16)

DIAGNOSIS.—Distinguished from all other *Negastrius* species by the strongly granulose pronotum; from *N. rupicola*, *N. choris*, *N. arnetti*, *N. atrosus*, *N. colon*, *N. solox*, *N. ornatus*, and *N. exiguus* by the anterior margin of elytra being nearly vertical in profile; and from *N. nadezhadae* and *N. delumbis* by the submarginal pronotal carina being longer than 0.5 length of pronotum.

DESCRIPTION.—Length (holotype 3.8 mm) 1.8–3.8 mm (mean = 3.6, s [standard deviation] = 0.5), width/length ratio 0.3–0.4 (mean = 0.4, s = 0.01); profile slightly arcuate; color rufous to black with a pale band on anterior third of elytra not extending mesally on interstriae 1 and extending to humerus on interstriae 5–8, each elytron also with a pale macula on posterior half.

Head and pronotum granulose; median line of pronotum distinctly elevated, especially on disc; some specimens with 2 smooth areas on middle of pronotum in sublateral areas; submarginal pronotal carina 0.6–0.8 times length of pronotum (mean = 0.7, s = 0.1); costa on

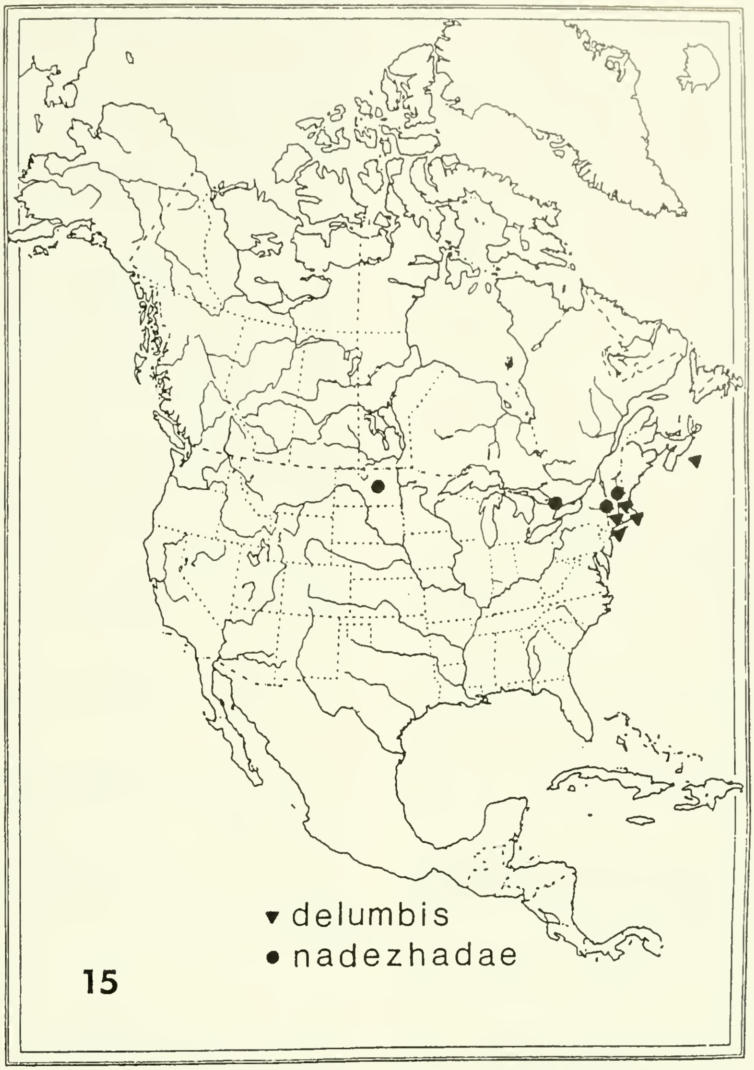


Fig. 15. Distribution of *Negastrius delumbis*, and North American distribution of *N. nadezhadae*.

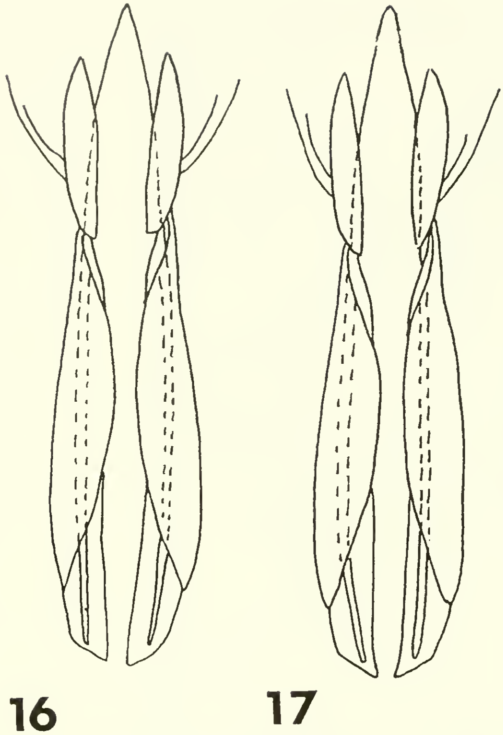
lateral margin of pronotum complete to anterior margin; rugosities on prosternal lobe slightly more pronounced than rugosities on remainder of prosternum; posterior margin of prosternum convex on lateral eighth; lateral margin of mesosternal fossa evenly concave; scutellum convex, anterior margin only slightly extended; outer angle of metatibia with 17–22 aligned setae (mean = 20.3, s = 1.8); anterior margin of elytra elevated almost 90 degrees in profile; interstriae on disc slightly punctate throughout.

HOLOTYPE.—Male and 11 paratypes from CALIFORNIA: Sutter Co., Nicalous, 25-VI-1944, A. T. McClay, deposited in the USNM, 1 paratype with same label is in the California Academy of Sciences. Paratypes include: BRITISH COLUMBIA: Oliver (1); Summerland (1). CALIFORNIA: Los Angeles Co. (1); Monterey Co. (12); Sacramento Co. (6); San Luis Obispo Co. (1); Santa Clara Co. (4); Santa Cruz Co. (2); Shasta Co. (1); Trinity Co. (5); Tulare Co. (2); Yolo Co. (2). MONTANA: Beaverhead Co. (1).

ETYMOLOGY.—Named in honor of Dr. J. N. L. Stibick, who has added greatly to our understanding of the Negastriinae and whose help was invaluable in this study.

BIOLOGY.—Some specimens were collected from flood debris.

DISCUSSION.—This species appears to be most closely related to the European species,



Figs. 16–17. Male genitalia of *Negastrius*: 16, *N. stibicki*; 17, *N. nadezhadae*.

N. sabulicola and *N. pulchellus*, but differs by the strongly granulose pronotum and by the pronotal carina being longer.

Negastrius rupicola, new species

(Fig. 13)

DIAGNOSIS.—Distinguished from all other North American species of *Negastrius* by the elevation of interstria 3; from *N. choris*, *N. arnetti*, *N. atrosus*, *N. solox*, *N. ornatus*, *N. colon*, *N. stibicki*, and *N. exiguus* by the posterior margin of the prosternum being convex on lateral sixth; and from *N. delumbis*, *N. nadezhadae*, and *N. stibicki* by the absence of elevation on the anterior margin of the elytra.

DESCRIPTION.—Length (holotype 2.4 mm) 1.8–3.4 mm (mean = 2.8, *s* = 0.4), width/length ratio 0.3–0.4 (mean = 0.4, *s* = 0.01); profile slightly arcuate; color black with 2 pale maculations on each elytron, 1 on humeral angle at base and 1 on posterior third.

Head and pronotum rugose to granulose; costa on anterior margin of pronotum thin; median line of pronotum smooth and slightly elevated to distinctly elevated; submarginal pronotal carina 0.45–0.78 times length of pronotum (mean = 0.6, *s* = 0.1); costa on lateral margin of pronotum complete to anterior margin; rugosities on prosternal lobe not more distinct than rugosities on remainder of prosternum; posterior margin of prosternum convex on outer eighth and becoming concave mesally; scutellum strongly convex, widening anteriorly; elytral interstriae finely punctate on disc, base of interstriae 3 distinctly raised above level of other interstriae; lateral margin of mesosternal fossa evenly concave; outer angle of metatibia with 12–19 aligned setae (mean = 15.9, *s* = 1.4).

HOLOTYPE.—Male and 17 paratypes from WASHINGTON: King Co., Northbend, 8-VII-1920, E. P. Van Duzee, deposited in the USNM. Paratypes include: BRITISH COLUMBIA: Bowser (1); Cowichan Lake (1); Hope (1); Keremeos (1); Salmo (1); Vancouver Island (1). CALIFORNIA: Humboldt Co. (4); Marin Co. (1); Mono Co. (1); Monterey Co. (6); Plumas Co. (3); Santa Cruz Co. (2); Shasta Co. (2); Sierra Co. (4); Sutter Co. (2); Trinity Co. (6); Yolo Co. (1). OREGON: Columbia Co. (1); Douglas Co. (4); Jackson Co. (1); Linn Co. (1); Wallowa Co. (1); Washington Co. (5); Yamhill Co. (1). WASHINGTON: King Co. (17); Lewis Co. (1); Snohomish Co. (1).

ETYMOLOGY.—The name *rupicola* is a compound from the Latin *rupes* meaning rock and *cola* meaning to cultivate.

Negastrius choris (Say)

(Figs. 7, 13)

Elater choris Say 1839:172 (Neotype, male; Lucedale, George Co. Mississippi; USNM). New designation.
Cryptohypnus choris; Candeze 1860: 81.
Hypnoidus choris; Blatchley 1910: 724, Leng 1920: 171, Schenkling 1925: 212.
Hypolithus choris; Dietrich 1945: 32.
Negastrius choris; Fattig 1951: 13, Stibick 1991: 6–7.

The neotype designation is made because of the loss of the holotype in Say's collection and to help define the species in comparison to *N. arnetti*, which has recently been described by Stibick (1991).

Negastrius atrosus, new species

(Figs. 8, 12)

DIAGNOSIS.—This species is distinguished from *N. delumbis*, *N. stibicki*, *N. rupicola*, *N. nadezhadae*, *N. exiguus*, *N. ornatus*, *N. solox*, and *N. colon* by the pointed anterior margin of the scutellum; and from *N. choris* and *N. arnetti* by its black color with 0, 2, or 4 maculations on the elytra.

DESCRIPTION.—Length (holotype 3.5 mm) 2.7–4.8 mm (mean = 3.7, *s* = 0.5), width/length ratio 0.4–0.4 (mean = 0.4, *s* = 0.02); profile slightly arcuate to elongate; body entirely black or with 1 pale spot on posterior third of each elytron, uncommonly with another similar spot on anterior third of each elytron.

Head and pronotum granulose to rugose; median line of pronotum distinctly narrowly ridged; submarginal pronotal carina 0.6–0.8 times length of pronotum (mean = 0.7, *s* = 0.4); costa of pronotal margin complete to base; rugosities on prosternal lobe not more distinct than rugosities on remainder of prosternum; posterior margin of prosternum convex on lateral eighth; scutellum pointed in center of anterior margin and concave distally from center to lateral edge; elytral interstriae often rugose and without punctations on disc, although interstriae 1 and 2 often with punctures; lateral margin of mesosternal fossa evenly concave; outer angle of hind tibia with 14–19 aligned setae (mean = 16.6, *s* = 1.6).

HOLOTYPE.—Male and 16 paratypes were collected from ONTARIO: Essex, Point Pelee, 8-VII-1931, W. J. Brown, and are deposited in the Canadian National Collection.

ETYMOLOGY.—The name *atrosus* is from the Latin adjective *atrans* meaning black or dark, and the adjectival suffix *-osus* indicating abundance.

DISTRIBUTION.—Paratypes include: ONTARIO: Essex, Point Pelee (19). QUEBEC: Brome (1); Portneuf, St. Augustine (1); Cap-Rouge (6).

Fleutiauxellus extricatus,
new combination

Hypnoidus extricatus Fall 1926: 191–192.
Negastrius extricatus; Stibick 1991: 10–11.

The species referred to by Stibick (1991) as *Negastrius extricatus* is most likely *N. nadezhadae*, which occurs in the same geographical area. Stibick's *N. extricatus* and *N. nadezhadae* both have yellow patches on the elytra, a declivous scutellum, and a raised humeral area. Since Stibick's publication, specimens labeled *N. extricatus* have been located and are now in Stibick's collection. These specimens belong to the genus *Fleutiauxellus*. A specimen of *Fleutiauxellus* fitting Fall's description of *N. extricatus* in Stibick's collection (personal communication) was collected from the type locality in Alaska and may be a type. Fall's description of *N. extricatus* is clear on several points. The apical 3 segments of the antennae extend past the hind angles of the thorax whereas *N. nadezhadae* has the antennae not attaining the hind angles. Fall also refers to an impressed vertex that is absent in all *Negastrius* species. Several specimens from Cornell (taken from the type locality of *F. extricatus*), the USNM, Chicago Field Museum, and the Canadian National Collection, all of which were taken from Alaska, fit Fall's description on all points and have the 2nd segment of the antennae reduced; this is indicative of the genus *Fleutiauxellus*.

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BIGHORN SHEEP RESPONSE TO EPHEMERAL HABITAT FRAGMENTATION BY CATTLE

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ABSTRACT.—We studied seasonal cattle grazing as an agent of ephemeral habitat fragmentation on a newly reintroduced population of California bighorn sheep (*Ovis canadensis californiana*) in Big Cottonwood Canyon, Idaho, 1988–89. We evaluated the hypothesis that bighorn sheep avoid cattle. We documented sheep response to the proximity to cattle by direct observation. The core areas used by bighorn and distances to escape terrain generally decreased as cattle moved closer to sheep. Likewise, sheep moved from cattle as cattle approached them. Severity of response we observed is in marked contrast with that reported for established bighorn populations, suggesting that newly reintroduced bighorn sheep are more highly sensitive to the presence of cattle.

Key words: bighorn sheep, cattle, disturbance, Idaho, Ovis canadensis.

Prior to the 20th century, California bighorn sheep were abundant in montane regions of the western United States (Van Dyke et al. 1986). However, since 1840 population numbers of bighorn sheep and their area of distribution have decreased (Cowan 1940, Buechner 1960). Disease, excessive hunting, activities associated with mining, human disturbance, and pressure from livestock for resources and space reportedly contributed to the extirpation of the subspecies from most of its range (Smith 1954, Geist 1971, Graham 1971, Demarchi and Mitchell 1973, Demarchi 1975, Trefethan 1975, Van Dyke 1978, Smith et al. 1988).

California bighorn sheep were once abundant in parts of southwestern Idaho; the last observations were recorded during the 1920s (Hanna 1978). The Idaho Department of Fish and Game (IFG) initiated reintroduction programs of returning California bighorn to parts of their historic range in 1963. Thirty-eight sheep from the Chilcotin River herd in British Columbia were transplanted into the drainages of the East Fork of the Owyhee River between 1963 and 1966 and have provided a base for subsequent reintroductions. In 1967, 12 additional bighorn were reintroduced into the nearby Little Jack's Creek drainage. Both populations were allowed to expand until 1980 (Toweill 1985). From 1980 to 1989, >100 sheep were relocated to 5 different regions in southern Idaho.

Livestock pressures have been heavy on rangelands in the western United States that historically supported populations of bighorn sheep (Mackie 1978). Seventy percent of the public land area in the 11 westernmost states is grazed at least seasonally. Within Idaho rangeland conditions varied. In 1986 surveys from the Owyhee range in Idaho reported 57% of the range in poor condition, 35% fair, and only 5% in good condition (Bureau of Land Management, Owyhee rangeland program summary, Burley District, ID, files, 16 pp., 1986); while in 1982, 30% of the range was in poor condition, 57% fair, and 18% in good condition (Bureau of Land Management, Twin Falls, land use decisions summary and rangeland program summary, Burley District, ID, files, 26 pp., 1982). Peiper (1988) reported that improvement in range condition has been slow since 1973.

Bighorn sheep are more sensitive to land uses associated with development than most native ungulates (Andryk and Irby 1986). Additionally, bighorn sheep are comparatively less abundant, react adversely to disturbance, and occupy habitats sensitive to change (Van Dyke et al. 1986). Livestock activities on these sites can negatively affect sheep through resource exploitation (i.e., forage, space, cover, water) or behaviorally (Geist 1971). On shared ranges social intolerance may impose greater limitations on distribution and habitat use of bighorn

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than competition for forage; however, biologists disagree whether livestock impact bighorn sheep spatial boundaries, limiting distribution. Wilson (1975) and Van Dyke et al. (1986) reported that bighorn show aversions to cattle and avoid them when unaccustomed to their presence on the range (Drewek 1970, Kornet 1978), while others did not detect reactions between sheep and cattle (King 1985, King and Workman 1985). Analyses that test the avoidance of livestock by bighorn sheep are limited.

Habitat fragmentation theory has application to seasonal livestock grazing. Habitat fragmentation may be permanent (e.g., subdivision construction) or ephemeral, as in seasonal livestock grazing. Effects of permanent fragmentation on habitat use have received increasing attention in recent years; however, less is understood about effects of seasonal fragmentation. We postulated that areas used by bighorn sheep are fragmented during spring and summer by cattle on grazing allotments. An area may appear large but, due to fragmentation, have a much smaller useable area. If bighorn sheep avoid livestock, the area available to them is reduced temporarily as livestock graze seasonally in sheep habitat, resulting in sheep exclusion from areas of potential use. A population may be influenced as sheep are restricted to smaller patches of habitat and effects of density dependence are felt. In our study we wanted to determine whether avoidance occurs, assess its effect on habitat use by sheep, and consider how avoidance, if it occurs, might influence future decisions for reintroductions.

STUDY AREA

We conducted the study in Big Cottonwood Canyon 16 km northwest of Oakley (Cassia Co.), Idaho. The canyon is approximately 18 km long, with Cottonwood Creek flowing to the northeast through the canyon bottom. Elevation of the canyon floor increases gradually from 1400 to 2100 m. Average elevation gain from the canyon floor to the mesa top is 365 m. Canyon walls are steep and characterized by a combination of cliffs, boulder slopes, grass, and shrub slopes. Woody vegetation includes four-wing salt brush (*Atriplex canescens*), spiny hopsage (*Grayia spinosa*), low sage (*Artemisia arbuscula*), horse brush (*Tetradymia canescens*), rabbit brush (*Chrysothamnus nauseosus*), bluebunch wheatgrass (*Agropyron spicatum*), and juniper (*Juniperus occidentalis*).

Big Cottonwood Canyon lies within the Sawtooth National Forest and contains a cattle grazing allotment that is leased from late May until early October. This grazing allotment consists of 5 pastures managed on a reverse-rotation basis and supports 400 cows with calves. Mesas south of the canyon contain another allotment of 3 pastures; this allotment is managed on a deferred-rotational system with 100 cows with calves. Permit dates for the Big Hollow allotment are late May to late October.

METHODS

Thirty-seven California bighorn sheep (19 with radio-collars, 18 with pattern-coded collars) were released into Big Cottonwood Canyon by the Idaho Department of Fish and Game during December 1986, December 1987, and November 1988. Collars marked with different designs in permanent ink allowed us to distinguish between non-transmittered individuals. The population at the beginning of our 1st summer field season (1988) was 23, 13 from the 1st reintroduction in 1986 and 10 from the 2nd in 1987. Fourteen additional sheep were released in November 1988.

We recorded daily locations of bighorn sheep by visual observation from May to September 1988 and June to September 1989. Telemetry was used only to aid in locating radio-collared bighorn sheep. We conducted weekly visual surveys to locate any uncollared sheep not close to collared individuals. Sheep were viewed from ≥500 m using a spotting scope to reduce chance of detection and disturbance. If we were detected and sheep movement followed, we disregarded subsequent observations of those individuals for the remainder of the day. Every effort was made to identify individuals within groups. We determined individuals by collar design or by telemetry frequency. Locations were recorded in Universal Transverse Mercator (UTM) coordinates. For each location we recorded group size and composition.

We defined escape terrain as broken habitat on which mountain sheep may safely outmaneuver or outdistance predators (Gionfriddo and Krausman 1985). Specifically, escape terrain may be characterized by a ruggedness index as defined by Beasom et al. (1983), and terrain class and number of cliff faces >120%

following Krausman and Leopold (1986). For every location we measured distance to escape terrain using a range finder once sheep left the area. We determined slope with a clinometer. We located cattle by hiking a systematic route on foot 3–4 times/wk. With the exception of group composition, data recorded for each cattle location were identical to sheep locations. We recorded cattle and sheep locations simultaneously allowing sheep movements to be analyzed in response to cattle movement for that specific time. Data not taken during identical time periods were not used in paired analyses.

Even though a controlled test was not possible, we wanted to observe the response of sheep when livestock were in proximity to sheep. On 14 August 1989, 5 cows were moved directly into an area of continuous sheep use and held continuously for 40 h. Cattle were kept within approximately a 0.8-km^2 area by 2 cowboys. Sheep response was observed and recorded. Cattle were watered every 5 h by removing them from the group one at a time and taking them to a trough in the bordering pasture. After 40 h all cattle were removed. We located sheep daily for the next 10 d.

We combined individual bighorn sheep locations for each group for analysis with Program Home Range (Samuel et al. 1985); thus, each location represented a group of bighorn sheep, not an individual. We used 95% harmonic mean measures of activity to estimate home ranges and core areas. We defined core areas as the maximum area where the observed utilization distribution as determined from the harmonic mean values was greater than a uniform utilization distribution (Samuel et al. 1985). Kolmogorov's test was used to determine if observed use was significantly ($P \leq 0.05$) greater than expected. All comparisons were considered significant at the 0.05 level. All data points were plotted at a scale of 1:12,000.

We recognize that harmonic mean measures have been criticized. Naef-Daenzer (1993) tested the spatial resolution of the conventional harmonic mean measure and a bivariate normal kernel estimator with a new kernel estimator he developed. The harmonic mean estimator generalized the distributions of 2 parallel gradients and estimated density at higher than zero for areas containing no sample points. Worton (1989, 1995) and Boulanger and White (1990) have outlined some undesirable properties of harmonic mean measures that were eliminated from kernel estimators using appropriate smoothing techniques. Specifically, with the harmonic measure, estimates of zero area can occur, and isopleths may include areas with no sample points (Worton 1995). We had no estimates of home range or core areas that approached or even came close to zero. Additionally, the isopleths we generated were based on tightly grouped locations of sheep, thus avoiding the problem of areas with no sample points. Finally, we did not employ interstudy comparisons, thus avoiding the onerous problem of comparing between methods, thereby reducing the effect of inherent bias.

We plotted mean monthly home ranges and core areas of sheep and cattle and then overlaid them to determine changes in size and location between consecutive months. We measured avoidance by quantifying changes in size and location of bighorn sheep range and core areas as cattle moved through bighorn sheep habitat. Changes in location were determined from harmonic means. We compared data collected during the 1st and 2nd field seasons to determine whether range and core areas were related to seasonal changes.

We calculated daily distances between bighorn sheep and cattle using UTM location coordinates. We defined consecutive locations as locations taken 1 d apart. Only cattle and bighorn sheep paired locations recorded at the same time were analyzed. Simple linear regressions were used to test for associations between 3 variables: distance (m) between cattle and bighorn, distance sheep moved in response, and distance from location of sheep to escape terrain. First, we tested sheep response to proximity of cattle; then we tested to determine whether distance between sheep and escape terrain was related to proximity of cattle.

RESULTS

Response of Bighorn Sheep to Cattle

Sheep range size did not change significantly in size or location ($P < 0.05$) from June to July in 1988 or 1989. Cattle were in adjacent pastures but because of topography were usually not visible to sheep or the observers. During August 1988, when cattle were moved to an allotment adjacent to areas receiving high sheep use, home range position shifted and range size decreased (Table 1). In September sheep expanded their range, coincident with

TABLE 1. Spatial responses of bighorn sheep in Little Cottonwood Canyon, Idaho, to the proximity of cattle.

Date	Range size (km^2)	Core area			Mean distance (m)		
		Size (km^2)	% use	% area[a]	c-s[b]	e-t[c]	Sheep[d]
6/88	13.4	4.3	61.4	32.1	4019	101	1616
7/88	13.7	4.7	53.9	27.3	4045	86	1246
8/88[e]	5.0	1.5	59.0	42.9	2251	55	1046
6/89	13.4	4.7	57.5	40.0	4820	112	1698
7/89	13.5	1.5	67.0	40.0	5148	63	1008
8/89[e]	7.2	1.5	55.6	40.0	3346	56	1276
		0.5[f]				11	

[a] Percent of total home range area that core area encompasses

[b] Mean distance between cattle and bighorn

[c] Mean distance of sheep to escape terrain

[d] Mean daily distance sheep moved during the month

[e] Cattle placed in allotments close to sheep

[f] Field experiment data

the movement of cattle during late August into a pasture adjacent to a high use sheep area. Sheep tended to concentrate into smaller core areas in 1988 and 1989 as proximity to cattle decreased.

No significant change (<3%) in core area of bighorn sheep occurred between July and August 1989 prior to moving cattle close to bighorn. When cattle were moved purposefully to within 800 m, bighorn sheep responded by immediately vacating the area and creating a new distinct core area. Distances moved by bighorn sheep directly after movement of cattle into the sheep core area were 355% greater than daily sheep movements during early August (3000 vs. 845 m, respectively). Sheep remained together and stayed within 35 m of escape terrain for the following 9 d. This was the longest time period during the study that sheep remained within 35 m of escape terrain. Distances between cattle and bighorn sheep remained >4000 m for the following 5 d.

Response of Bighorn Sheep Relative to Escape Terrain

As mean daily distance between cattle and sheep decreased, the mean distance between sheep and escape terrain tended to decrease. Core-area size appeared to be directly related (adjusted $r^2 = 0.81$) to distance to escape terrain (Fig. 1); the closer to escape terrain, the tighter sheep grouped together. A correlation matrix, generated from these spatial data, adds further corroboration for the association (Table 2). The mean daily distance that bighorn moved during the month was positively correlated ($r^2 = 0.88$) with increasing distance of sheep to escape terrain.

DISCUSSION

Hicks and Elder (1979) suggested that bighorn sheep were more likely to move greater distances when cattle were close, but were less likely to relocate when cattle were distant. Our data show increased movement by bighorn sheep as cattle moved closer. When we moved cattle to within 800 m, bighorn left the area. Sheep response to cattle was much more extreme than at any other time or when compared to their behavior when confronted by humans at other times during the field season. We were unable to differentiate between the effect that cattle had and the potential effect of the personnel involved. We do not doubt that personnel moving the cattle had an effect. Furthermore, the presence of both cattle and personnel close to sheep may well have augmented bighorn response nonlinearly. However, at other times when we accidentally alerted sheep during the study ($n = 10$), bighorn responded by relocating much shorter distances (between 872 and 1190 m). Additionally, their response was typically short-lived and they left the proximity of escape cover by the next day or sooner. Although both the proximity of cattle and personnel influenced bighorn response, the important point is that extreme proximity evoked a highly charged response. Even without our intentional movement of cattle toward sheep, their increasing affinity for escape cover as cattle moved closer suggests strongly that livestock were perceived as a threat.

Escape terrain is an important component of good sheep habitat (McQuivey 1978, Leslie and Douglas 1979, Weyhausen 1980, Krausman and Leopold 1986). We would have predicted

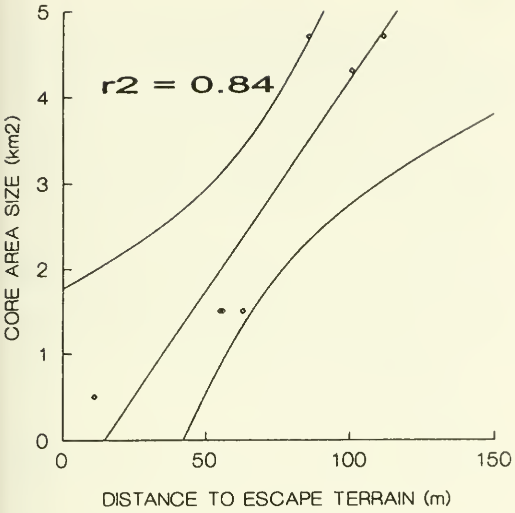

Fig. 1. Relationship between size of core area of bighorn sheep, Cottonwood Canyon, Idaho, and distance to escape terrain, 1988–89.

that tighter grouping should result as sheep moved farther from escape cover. However, our data show the direct opposite result, suggesting that when sheep move farther from escape terrain, they do so under less threatening situations. Selective pressures under these conditions appear not to result in tighter groups.

The response of bighorn sheep to cattle we observed is in contrast with bighorn sheep in national parks. In some parks sheep approached humans closely and were photographed from car windows (Van Dyke et al. 1986). Smith (1954) reported sheep eating from his hand, whereas others reported that sheep unaccustomed to people or cattle fled at the sight of humans or vehicles >1600 m (Van Dyke et al. 1985). It appears that newly reintroduced sheep are more sensitive to disturbance, perhaps resulting from recent transplant activities, and react differently than do established, undisturbed populations. Sheep reintroduced into Big Cottonwood Canyon were net-gunned from helicopters, blindfolded, and flown to a base. They then had blood drawn, were given inoculations, weighed, measured, placed into the back of a covered pickup with several conspecifics, and then transported approximately 160 km and kept overnight in the vehicles. All were released the following morning into an area foreign to them. As a result of exposure to such activities, any disturbance may more likely be viewed as a threat. In the Big Cottonwood Canyon population, alert-alarm behavior appears to be reinforced yearly with each new group of reintroduced animals. Age may also play a part; 55% of individuals released were <2 years of age. Heightened sensitivity and subsequent frequent reinforcement of alert behaviors appear to characterize the population and may be a general phenomenon for newly reintroduced populations placed into new areas. Sensitivity of these populations to disturbance may diminish over time as populations become established.

Avoidance has implications for reintroductions of bighorn sheep. The total area of potential habitat may not be used by sheep if livestock are present. If cattle allotments remain in use, it would appear wise to consider the possibility of ephemeral fragmentation by cattle when goals for desired bighorn population sizes are developed. Goals should be consistent with total useable habitat. Control of disturbance for recently reintroduced populations of bighorn sheep is certainly appropriate.

TABLE 2. Correlation matrix for home range, core area, and mean distance variables for bighorn sheep in Big Cottonwood Canyon, Idaho, 1988–89.

		Core area			Mean distance (m)		
	Range size	Size	% use	% area[a]	c-s[b]	e-t[c]	Sheep[d]
Range size	1.0	0.694	0.234	–0.601	0.887	0.721	0.440
Size		1.0	–0.380	–0.704	0.385	0.916	0.765
% use			1.0	0.335	0.410	–0.144	–0.272
% area				1.0	–0.220	–0.458	–0.266
c-s					1.0	0.520	0.308
e-t						1.0	0.887
Sheep							1.0

[a] Percent of total home range area that core area encompasses
[b] Mean distance between cattle and bighorn
[c] Mean distance of sheep to escape terrain

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A FIELD STUDY OF THE NESTING ECOLOGY OF THE THATCHING ANT, *FORMICA OBSCURIPES* FOREL, AT HIGH ALTITUDE IN COLORADO

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ABSTRACT.—A field study of the thatching ant, *Formica obscuripes* Forel, at 2560 m elevation in Colorado provided information on mound density, composition, dimensions, and temperatures; worker longevity; and mite parasitization. Density was 115 mounds/ha. Mounds had 1–52 entrances and *Peromyscus* fecal pellets in the thatch. Mounds conserved heat and exhibited thermal stratification. Excavations of 4 nests revealed depths of 0.3 m to almost 1 m, novel myrmecophiles, and 0–198 wingless queens per nest. Marking experiments demonstrated that some workers overwinter and live more than a year.

Key words: Formica obscuripes, *thatching ant, Colorado, ant mounds, myrmecophiles.*

Formica obscuripes Forel is in the *Formica rufa*-group (Weber 1935) and ranges from Indiana and Michigan westward across the United States and southern Canada. It is one of the most abundant ants in western North America, especially in semiarid sagebrush areas (Gregg 1963), and has been found at altitudes up to 3194 m (Wheeler and Wheeler 1986).

The objective of this field study was to compare mound density, formation, composition, dimensions, and temperatures, worker longevity and parasitization, nest depths, myrmecophiles, and the number of wingless queens per colony of this species at high altitude in Colorado with findings from lower altitude studies in Colorado (Jones 1929, Gregg 1963, Windsor 1964), Idaho (Cole 1932), Iowa (King and Sallee 1953, 1956), Michigan (Talbot 1972), Nevada (Clark and Comanor 1972, Wheeler and Wheeler 1986), North Dakota (McCook 1884, Weber 1935), Oregon (McIver and Loomis 1993, McIver and Steen 1994), Washington (Henderson and Akre 1986), and Canada (Bradley 1972, 1973a, 1973b). Although this species seems to be most common at altitudes of 1524–2743 m in the mountainous states (Gregg 1963, Wheeler and Wheeler 1986), the highest previous study site was at an elevation of 1550 m (Clark and Comanor 1972). It is hypothesized that climatic and vegetational changes associated with higher altitude may alter the nest ecology of this species.

MATERIALS AND METHODS

The study site is in Gunnison County north of Blue Mesa Reservoir and west of Soap Creek Co. Rd. in western Colorado at an altitude of 2560 m. Field observations were conducted 5–6 August 1990, 20 June –11 October 1992, 28 June–16 August 1993, 29 June–31 July and 14–16 August 1994, and 3, 29–31 July and 15–16 August 1995. The area, dominated by big sagebrush (*Artemesia tridentata* Nuttall) and to a lesser extent by rubber rabbitbrush (*Chrysothamnus nauseosus* [Pallas] Britton), is adjacent to a grove of quaking aspens (*Populus tremuloides* Michaux).

The locations of 85 mounds were mapped in a study area (64.6 m × 114 m) using a surveyor's transect and compass in July 1993 to determine density.

The diameters and heights of 97 mounds in the study area and surrounding area were measured. The number of entrances per mound was determined by inserting sprinkler flags into the active openings on each mound.

Mound temperatures were measured with a Model 100-A VWR digital thermometer probe. Sixty-seven temperature measurements were made on 34 mounds in the evenings (1915–2045 h) 2–14 July 1993 by inserting the probe approximately 15 cm into the top of each mound. The temperatures of 4 of these mounds were also recorded in the afternoon (1538–1600 h)

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on 2 July 1993. In addition, hourly temperatures were recorded at 4 locations (air, ground, mound top, and mound base) for 3 different-sized mounds in July 1994 between 0700 and 2000 h to determine how mound size affects thermal dynamics. Temperatures were taken at a mid-sized mound (height = 25.4 cm, average diameter = 1 m) on 16–18 July, at a large mound (height = 49.5 cm, average diameter = 1.21 m) on 18 July, and at a small mound (height = 27.9 cm, average diameter = 0.51 m) on 17 July. The small and mid-sized mounds were about 4.6 m apart and about 34–37 m from the large mound. The probe was inserted approximately 15 cm into the top, base, and ground adjacent to each mound. Temperatures were also recorded in the shade about 15 cm above the ground near each mound.

Hundreds of workers were marked on 8 mounds and 5 plants in 1992–93 by applying model airplane paint with a fine-tipped brush and by spraying 5 mounds in 1994 with colored acrylic enamel. Although many workers were incapacitated or killed, especially by spraying, most survived. Spraying was the most efficient technique for marking large numbers of ants.

Four nests were excavated, 1 each on 6 August 1990, 27–28 June 1992, 12 July 1993, and 11–25 July 1994. The 1993 nest was poisoned with 1½ cups Hi-Yield ant killer granules (Diazinon) wetted down with about 7.6 L of water prior to excavation to investigate another technique for collecting queens and myrmecophiles.

RESULTS

Nest Density

The extrapolated density for the 85 mounds mapped in the 7364-m^2 area was 115 mounds/ha. The closest mounds were 2.36 m apart.

Mounds

FORMATION AND COMPOSITION.—Mounds are composed of thatch and are usually dome shaped. Some mounds are exposed while others are overgrown or shaded by low vegetation. Dead sagebrush protruded from or was found on 63 of 98 mounds (64%). The largest mound was built around the base of a fence post. No mounds were found inside the aspen grove, but 2 were built around small aspen trees on the forest edge.

Mound thatch consisted mainly of twigs but also contained fecal pellets, probably from the deer mouse (*Peromyscus maniculatus* [Wagner]) or vole (*Microtus* sp.). Thatch (n = 58) from 1 mound consisted mainly of small twigs 4–89 mm (mean = 24.19 mm) long and 1–5 mm (mean = 2.19 mm) in diameter. Workers were observed carrying fecal pellets into or out of mound entrances, but not on trails.

DIMENSIONS AND ENTRANCES.—The diameters of 97 mounds ranged from 19 cm to 142 cm (mean = 65 cm). Mound heights ranged from 6 cm to 58 cm (mean = 26 cm).

The number of entrances to 97 mounds ranged from 1 to 52 per mound (mean = 12), but their number, size, position, and activity changed over time. For example, 1 mound had 10 or more entrances in August but only 2 in October. Some entrances were larger than others, and some surrounded plant stalks growing out of mounds.

TEMPERATURES.—Measurements of mound-top and air temperatures in July 1993 demonstrated that mounds are warmer than air temperatures and that the differential is greater in the evening than in the afternoon. Evening temperatures (n = 67) for 34 mounds were 1.0°–15.5°C (mean = 8.6°C) warmer than corresponding air temperatures. Afternoon temperatures for 4 of these mounds were slightly warmer (0.5°–0.9°C; mean = 0.7°C) than corresponding air temperatures.

Hourly mound-top and mound-base temperatures recorded in July 1994 were almost always higher than ground temperatures, and top temperatures were warmer than air temperatures (Figs. 1–3). Differences in top and air temperatures were greater in the evening (1900–2000 h) for a large nest (8.9°–11°C) and mid-sized nest (6.8°–14.4°C) than their afternoon (1500–1600 h) differences, 2.6°–6.3°C and 0.6°–8°C, respectively. On the other hand, hourly top and air temperatures did not differ much for the small nest in the evening (1.1°–3.3°C) and in the afternoon (1.6°–2.2°C).

Average hourly top and base temperatures were higher than average air temperatures for the mid-sized and large mounds (Figs. 1–3). For example, average top and base temperatures were 6.2°C and 3.1°C higher than average air temperatures for the large mound and 4.6°C and 0.5°C higher for the mid-sized mound. However, for the small mound the average top temperature was actually 0.8°C lower, whereas the average base temperature was 2.7°C higher than the average air temperature.

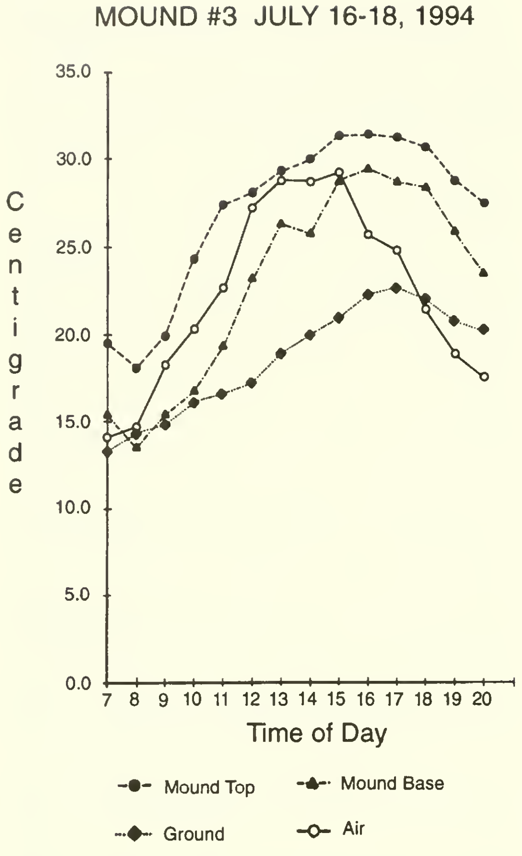

Fig. 1. Average mound-top, mound-base, ground, and air temperatures around a mid-sized *Formica obscuripes* mound from 0700 to 2000 h on 16–18 July 1994 at 2560 m in Colorado.

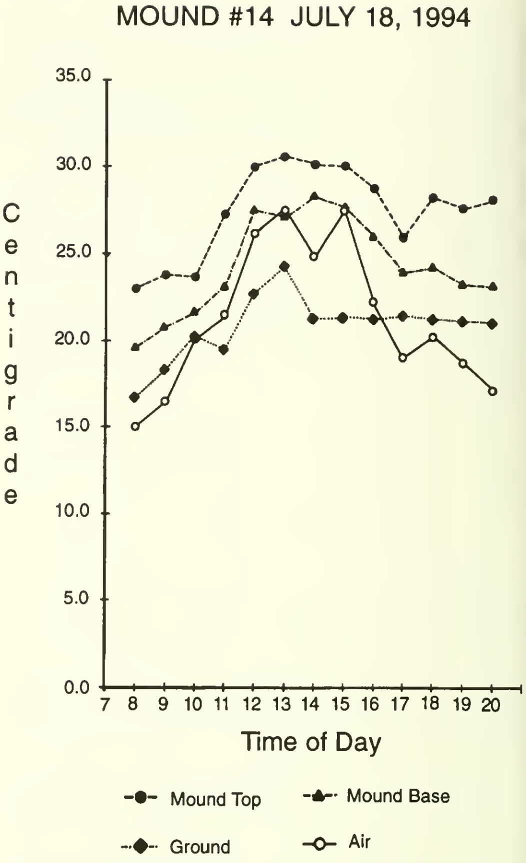

Fig. 2. Mound-top, mound-base, ground, and air temperatures around a large *Formica obscuripes* mound from 0800 to 2000 h on 18 July 1994 at 2560 m in Colorado.

Hourly top and base temperatures showed thermal stratification. Average top temperatures were 3.2°C and 4.1°C higher than average base temperatures for the large and mid-sized mounds, respectively. However, for the small mound the stratification was reversed: average top temperature was 3.5°C lower than the average base temperature.

The poor thermal regulation of smaller mounds was also reflected by a greater fluctuation of hourly top and base temperatures. Daily ranges of top/base temperatures were 7.6/8.7°C, 13.3/15.9°C, and 13.8/26.3°C for the large, mid-sized, and small nests, respectively. Thus, larger mounds exhibited less daily temperature fluctuation than smaller mounds.

Worker Longevity

Most marking experiments ($n = 14$) indicated that some workers live 19 to 44 d (mean = 31.6 d). However, 2 workers marked on a mound between 7–9 July and 15–27 July 1994, respectively, were observed on 30 July 1995 on another mound and on the original mound. Thus, some workers overwinter and live more than 1 yr.

Mites

Mite infestation was not common. Orange, spherical mites were noted on only 1 worker at 3 of the many mounds observed. The largest number of mites observed was 4–5 on the thorax and gaster of 1 worker.

Excavated Nests

Each of the 4 nests excavated contained numerous workers, larvae, and pupae, but the number of wingless queens per nest varied greatly: 0, 1, 32, and 198. No winged reproductives were found except a male in 1 nest. The

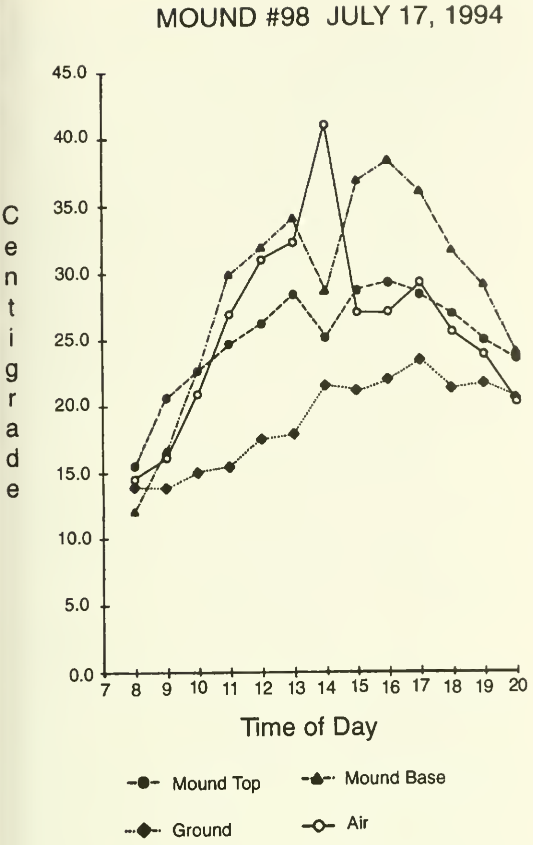

Fig. 3. Mound-top, mound-base, ground, and air temperatures around a small *Formica obscuripes* mound from 0800 to 2000 h on 17 July 1994 at 2560 m in Colorado.

depths of the nests were 0.3 m (estimated), 0.3 m, 0.64 m, and 0.97 m.

The nest excavated in 1993 contained the following arthropods: pseudoscorpions, collembolans, beetles and beetle larvae (1 *Ctenicera* sp. [F. Elateridae] and 4 *Eleodes* sp. [F. Tenebrionidae]; Table 1).

The following insects were identified in the 1994 nest: Collembola (F. Entomobryidae); Homoptera (F. Cicadellidae—1 immature, F. Aphididae—2 immatures); Hemiptera (F. Anthocoridae—1 specimen); Coleoptera (F. Curculionidae—5 adults, F. Scarabaeidae—1 adult and *Cremastocheilus* pupa and larval skin, probable F. Carabidae—1 adult, probable F. Anthribidae—2 larvae, F. Tenebrionidae—unidentified larvae, probable *Eleodes* sp. larvae, and *Eleodes* sp. pupae, F. Cerambycidae—Lepturinae, probable *Leptura* sp. larva); Diptera (probable F. Asilidae—pupa); Hymenoptera (F. Formicidae—few *Tapinoma sessile* [Say] workers); and Lepidoptera (F. Noctuidae—larvae; Table 1).

DISCUSSION AND CONCLUSIONS

The extrapolated density of 115 mounds/ha is about 1.8 times greater than the highest density reported: 64/ha of Jack pine in Manitoba (Bradley 1973a).

Colonies are known to be polydomous and to reproduce by budding (Herbers 1979). Some primary mounds and small secondary moundlets along trails appeared and disappeared in our study area over the years as previously reported, and some may have moved. For example, a primary mound that was active in 1990 was largely deserted by 1994 and completely abandoned in 1995. Colonies have been reported to move at least 3 times during their life and to move 18 m from their original location, or 1.3–33 m after transplantation (Bradley 1972, 1973a). King and Sallee (1953, 1956) noted desertions of many old nests and the establishment of 1 or more new ones from each of them.

All our mounds were in open sagebrush except for 2 built around aspens at the forest edge. Weber (1935) also noted that most mounds are in the open, but did find some mounds partially shaded and 1 enormous mound almost completely shaded in an aspen grove.

In our study, 63 of 98 mounds (64%) showed evidence of being built around sagebrush as reported by Weber (1935), but a few were built around other structures such as trees and a fencepost. Weber noted that workers kill sagebrush by chewing bark at the base and spraying formic acid on the cambium. After 3 months, the stem is removed to form a longitudinal passage in the center of the mound leading to the main entrance.

Weber (1935) reported that mounds are composed of slightly longer twigs (1–12 cm) than the ones we measured (0.4–8.9 cm), but these slight differences may simply reflect the availability of materials.

A new discovery was the presence of fecal pellets of *P. maniculatus* or *Microtus* (Clark personal communication) on the surface and in the thatch of Colorado mounds. Since workers were never observed carrying pellets to mounds, their origin is unclear.

Although Clark and Comanor (1972), Talbot (1972), and Wheeler and Wheeler (1986)

TABLE 1. Arthropods in *Formica obscuripes* Forel nests reported in the literature and identified from 2 excavated nests near Soap Creek, Colorado (*).

*Collembola (unident.)	Weber (1935)
*F. Entomobryidae	
*Homoptera	
*F. Aphididae—2 immatures	
*F. Cicadellidae—1 immature	
*Hemiptera	
*F. Anthocoridae—1 specimen	
Diptera	
*F. Asilidae—pupa	
F. Milichiidae	
Phyllomyza securicornis	Weber (1935)
F. Leptidae—larvae	Weber (1935)
F. Anthomyiidae—larvae	Weber (1935)
F. Therevidae—larvae	Weber (1935)
F. Phoridae—larva	Windsor (1964)
Lepidoptera	
*F. Noctuidae—larvae	
Epizeuxis sp.—larvae	Weber (1935)
Hymenoptera	
F. Formicidae	
Lasius latipes Walsh	Weber (1935)
Leptothorax hirticornis Emery	Weber (1935)
**Tapinoma sessile* Say	Weber (1935)
Thysanura—silverfish	Windsor (1964)
Coleoptera	
Unident. beetle pupa	Windsor (1964)
F. Elateridae	
**Ctenicera* sp. larva	
Melanotus sp. larvae	Weber (1935)
F. Tenebrionidae	
Unident. larvae and adults	Windsor (1964)
**Eleodes* sp.—larvae and pupae	
*Unident. larvae	
F. Carabidae	
Amara sp.—adult female	Weber (1935)
*Prob. adult	
Unident. adults	Windsor (1964)
*F. Anthribidae	
*2 prob. larvae	
*F. Cerambycidae	
*Prob. *Leptura* sp.—larva	
*F. Curculionidae	
*5 unident. adults	
Coleoptera (continued)	
F. Scarabaeidae	
*Unident. adult	
**Cremastocheilus* sp.—pupa and larval skin	
Cremastocheilus wheeleri Le Conte—larvae	Windsor (1964)
Cremastocheilus wheeleri Le Conte—adults	Windsor (1964)
Unident. pupae	Weber (1935)
Euphoria inda L. in pupal cells	Weber (1935)
Euphoria inda L. larvae	Windsor (1964)
Euphoriaspis hirtipes (Horn)—larvae and adults	Windsor (1964)
Serica intermixta Bltch.—adults	Weber (1935)
Phyllophaga spp.	Weber (1935)
F. Staphylinidae	
Tachyporus californicus	Mann (1911)
Philonthus agilis Grav., *P. debilis* Grav., *P. thereneti* Horn	Weber (1935)
Goniusa alperti Kistner	Mackay & Mackay (1984)
Goniusa obtusa Lec.	Weber (1935)
Aderocharis corticinus Grav.	Weber (1935)
Paederinae (*Gastrolobium* or related genus)	Weber (1935)
Platymedon laticollis Csy.	Weber (1935)
Small unident. adults	Windsor (1964)
F. Chrysomelidae	
Cryptocephalus sp.—larvae	Weber (1935)
F. Hydrophilidae	
Berosus sp.	Weber (1935)
F. Cryptophagidae	
Atomaria sp.	Weber (1935)
F. Histeridae	
Hetaerius adult	Weber (1935)
F. Anthicidae	
Anthicus sp.—adult	Windsor (1964)
Orthoptera	
F. Gryllidae	
Myrmecophila manni Schimmer	Henderson and Akre (1986)
Arachnida	
Small gray spiders	Windsor (1964)
*Pseudoscorpionida	

reported mound diameters within the range we observed (9–142 cm), Weber (1935) noted a much greater range (13–335 cm), but a smaller mean diameter (43 cm) than we found (65 cm).

Talbot (1972), Clark and Comanor (1972), and Wheeler and Wheeler (1986) noted mound heights in the range we measured (6–58 cm), but Weber (1935) reported lower heights (2.5–46 cm) and Henderson and Akre (1986) reported mounds up to 1.22 m high. Somewhat lower (20 cm) and higher (30 cm) mean heights were recorded by Weber (1935) and Wheeler and Wheeler (1986), respectively, than we found (26 cm).

The number, size, position, and activity of mound entrances changed over time as reported by Weber (1935). The number of entrances per mound in our study, 1–52, is close to the range of 3–50 per mound reported (Cole 1932, Wheeler and Wheeler 1986). In the early morning ants use openings in the sunlight; later as the temperature rises they use only shaded entrances as reported by Weber (1935). Henderson and Akre (1986) speculate entrances are opened during the day and closed with thatch at night to help control nest temperatures.

Our mounds, especially mid-sized and large ones, were generally warmer than ground and air temperatures and exhibited thermal stratification from top to base. Weber (1935) and Andrews (1927) also noted that mounds are warmer than the ground, and Andrews reported that the upper parts are warmer than the lower parts of mounds. The differential between our mound-top and air temperatures was greater in the evening than in the afternoon. Small mounds showed a reversal of thermal stratification and greater hourly fluctuation of top and base temperatures, which is indicative of poorer thermal regulation.

Marking experiments suggest that worker longevity is often short but that some workers overwinter and live more than a year. Little information is available on the longevity of worker ants and none was found for this species. Although maximum longevity is known to be 3 yr for workers of some species, such as *Aphaenogaster rudis* (Emery), for others, such as *Solenopsis invicta* Buren, it is only 10–70 wk (Hölldobler and Wilson 1990).

Mites were found on only 3 workers in our study area. Weber (1935), on the other hand, noted that mites (Parasitidae, Tyroglyphidae, *Uropoda* sp.) were common on workers and sexuals, especially on the tibia-tarsal joint, and estimated over 200 on 1 queen.

Excavated nests varied in depth from 0.3 to 0.97 m, or less than the maximum depth of 1.37 m noted by McCook (1884) and 1.58 m reported by Weber (1935). Weber speculated that the water table (below 1.52 m) limits nest depth.

Nests excavated from 27 June to 6 August did not contain winged reproductives except a male in 1 nest. This finding differs from Cole's (1932) observations of large numbers of winged reproductives through June and July.

Many species of *Formica* are polygynous (Kannowski 1963). The number of wingless queens per Colorado nest varied from 0 to 198 (Conway 1996). The latter number far exceeds the 2 or more queens per colony reported by Cole (1932).

The following arthropod groups found in our excavated nests had not been reported associated with this species: pseudoscorpions, collembolans (F. Entomobryidae), homopterans (F. Aphididae, F. Cicadellidae), hemipterans (F. Anthocoridae), dipterans (F. Asilidae), and coleopterans (F. Carabidae, F. Anthribidae, F. Curculionidae, F. Elateridae—*Ctenicera* sp., F. Tenebrionidae—*Eleodes* sp., and F. Cerambycidae—probable *Leptura* sp.; Table 1).

On the other hand, Windsor (1964) and Henderson and Akre (1986) reported 3 major groups not found in our limited sampling: Arachnida (small spiders), Thysanura (silverfish), and Orthoptera (F. Gryllidae). In addition, Weber (1935), Windsor (1964), and MacKay and MacKay (1984) noted many dipteran and coleopteran families not in our nests and new genera and species in a few of the same families found in our nests (Table 1).

The relationship of these myrmecophiles with the host colony is unclear. Larval and adult coleopterans and noctuid larvae may use the chambers for hibernation or development (Weber 1935). Staphylinid beetles may prey upon brood or workers. Jones (1929) suggested that lepidopteran, coleopteran, and dipteran larvae are tolerated because they feed on decaying vegetable matter in the nest. *Cremastocheilus* is a well-known symbiont in the nests of a number of ant species (Hölldobler and Wilson 1990). The scarab genus *Euphoria* may be a symbiont treated with indifference by the host colony (Wheeler 1910). On the other hand, ants are aggressive to other guests, such as the myrmecophilous cricket (*Myrmecophila manni* Schimmer; Henderson and Akre 1986).

Weber (1935) reported 3 ant species in nests (Table 1) and noted that *Leptothorax hirticornis* Emery may prey upon brood or isolated workers. *Tapinoma sessile*, one of the species in our nests, often steals honeydew from thatching ants throughout its territory, but seems to elicit little defensive response (McIver and Loomis 1993).

The high altitude of our study site did not seem to significantly alter nest dimensions and ecology, but the work did provide new findings on this species, such as the greatest mound density per hectare, first report of probable *P. maniculatus* fecal pellets associated with mound thatch, new information on the thermal properties of mounds, new information on worker longevity, greatest number of wingless queens reported in a nest, and possible new myrmecophiles.

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GAS EXCHANGE, δ^{13}C, AND HETEROTROPHY FOR *CASTILLEJA LINARIIFOLIA* AND *ORTHOCARPUS TOLMIEI*, FACULTATIVE ROOT HEMIPARASITES ON *ARTEMISIA TRIDENTATA*

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ABSTRACT.—Gas exchange and carbon isotope ratios were measured on 2 facultative hemiparasites, *Castilleja linariifolia* Benth. (Indian paintbrush; Scrophulariaceae) and *Orthocarpus tolmiei* H. & A. (Tolmie owl clover; Scrophulariaceae), and their *Artemisia tridentata* L. (big sagebrush; Asteraceae) hosts. Photosynthetic rates differed greatly between years; rates in 1995 were more than double those in 1994, likely due to more precipitation and less water stress during 1995. Despite this difference in precipitation, photosynthetic rates for *C. linariifolia* were not different from those of their hosts for either year. However, carbon isotope ratios of *C. linariifolia* and *O. tolmiei* were up to 3‰ more negative than those of their *A. tridentata* hosts. Using measured δ^{13}C ratios in conjunction with δ^{13}C ratios predicted from gas-exchange measurements, we calculated that *C. linariifolia* derived, on average, 40% of its leaf carbon heterotrophically. Contrary to current suggestions that high photosynthetic rates of hemiparasites are an indication of reduced heterotrophy, *C. linariifolia* exhibited photosynthetic rates similar to autotrophic plants and used a substantial amount of host-derived carbon. Moreover, this evidence shows that manipulation of a heterotrophic carbon supply transcends obligate hemiparasites to include those plants whose parasitism is facultative.

Key words: heterotrophy, hemiparasite, photosynthesis, carbon isotope ratios, shrub ecology.

Hemiparasites, chlorophyllous parasitic plants, form an apoplastic continuum with host xylem (Raven 1983). It has been assumed that these plants are largely autotrophic plants, being parasitic only for water and minerals (Smith et al. 1969). However, hemiparasites may also gain carbon through the passive uptake of dilute concentrations of organic carbon contained within host xylem sap (Raven 1983). Early studies using radiocarbon labeling demonstrated the transfer of solutes from host to parasite (Hull and Leonard 1964, Govier et al. 1967), although it was not possible to quantify this flux. Experiments of Govier et al. (1967), in which [^{14}C]urea or $^{14}CO_2$ was fed to hosts, showed the movement of ^{14}C labeled compounds to all parts of the hemiparasite *Odontites verna* (Scrophulariaceae). More recent studies used a carbon budget model and/or a δ^{13}C method to quantify the extent of heterotrophy (Press et al. 1987a, Graves et al. 1989, Marshall and Ehleringer 1990, Schulze et al. 1991, Marshall et al. 1994, Richter et al. 1995). Using the latter method, Press et al. (1987a) calculated that 28–35% of total carbon in *Striga hermonthica* and *Striga asiatica* (Scrophulariaceae) is host-derived carbon. There is also ample evidence that hemiparasitic mistletoes utilize host-derived carbon, although the values vary greatly, from 5% to over 60% (Marshall and Ehleringer 1990, Schulze et al. 1991, Marshall et al. 1994, Richter et al. 1995). Despite the potential importance of heterotrophy to carbon acquisition in parasitic plants, relatively few studies have addressed this aspect of parasite-host interactions. Moreover, none have evaluated the exploitation of this carbon source by facultative root hemiparasites.

Photosynthetic rates of hemiparasites fall within the lower range reported for C_3 plants and are generally much lower than photosynthetic rates of the host. *S. hermonthica* has a poorly developed palisade mesophyll, contributing, in part, to photosynthetic rates as low as 2.5 μmol m^{-2} s^{-1} (Shah et al. 1987). Moreover, these rates are half those reported for their *Sorghum* hosts (Press et al. 1987b). *Striga* species are the most extensively studied root hemiparasites because of their importance as agricultural weeds in semiarid Africa, and as obligate hemiparasites they require host attachment for survival. Similarly, low photosynthetic rates were found in facultative root hemiparasites. Press et al. (1988) measured light-saturated photosynthetic rates of 2.1 to 7.5 μmol m^{-2} s^{-1} for 8 facultative species of Scrophulariaceae. However, 1 exception to this trend of low photosynthetic rates is the Mediterranean facultative hemiparasite *Bartsia trixago* (Scrophulariaceae), which has CO_2 assimilation rates ranging from 12.4 to 18.8 μmol m^{-2} s^{-1}, well within the range measured for potential hosts (Press et al. 1993).

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Castilleja and *Orthocarpus* are facultative hemiparasites, those with the ability to survive in the absence of a host. It is this facultative parasitism that distinguishes them from *Striga.* The majority of *Castilleja* species are perennial, while *Orthocarpus* are annuals. Both occur throughout the Intermountain West most commonly in the pinyon-juniper, mountain brush, and aspen-conifer zones (1140–3140 m elevation), with *Orthocarpus tolmiei* occurring only at the higher elevations (2195–3265 m; Welsh et al. 1987). *Castilleja linariifolia* and *Orthocarpus tolmiei* parasitize a variety of host species (Heckard 1962, Atsatt and Strong 1970). *Artemisia tridentata* is the common host for both hemiparasites at the sites studied in the paper.

Our overall objective was to investigate gas exchange and heterotrophy characteristics for facultative hemiparasites. We focused primarily on the facultative root hemiparasite *Castilleja linariifolia* infecting *Artemisia tridentata* hosts. A secondary focus of this study was *Orthocarpus tolmiei,* a closely related annual facultative root hemiparasite, also infecting *A. tridentata* hosts. We asked the following questions: Do *C. linariifolia* and *O. tolmiei* exhibit gas-exchange activities similar to those of their hosts? Does *C. linariifolia* utilize heterotrophic carbon? Does hemiparasite infection impact water availability and gas-exchange rates of *A. tridentata* hosts? To evaluate these questions, we measured gas exchange and analyzed carbon isotope composition for *C. linariifolia, O. tolmiei,* infected and uninfected *A. tridentata.* In addition, predawn water potentials (Ψ_{pd}) were measured for infected and uninfected *A. tridentata* to examine the impact of hemiparasite infection on host water availability.

MATERIALS AND METHODS

Study Sites

This study was conducted at 2 sites in Utah where the hemiparasites have different growing seasons. The first site, Tintic, is located just off McIntyre Road, approximately 12 km south of Eureka, Utah (Juab Co.), at the Desert Range Experimental Station operated by Utah State University (latitude 39°51′N, longitude 112°12′W). The area is a sagebrush steppe habitat at about 1525 m elevation where sagebrush is interspersed with herbaceous species such as *Erigeron, Castilleja, Astragalus,* and *Phlox.* The growing season for *Castilleja* at this site begins in late April and ends in late June to early July. The second site, Strawberry Reservoir (Wasatch Co.), is about 130 km southeast of Salt Lake City and approximately 800 m north of Highway 40 along Coop Creek Road (latitude 40°15′N, longitude 111°8′W). This site lies in the southern tip of the Uinta National Forest at about 2280 m elevation. Sagebrush is the dominant shrub mixed with a few herbaceous species such as *Castilleja, Orthocarpus,* and *Malva.* The growing season for *C. linariifolia* at Strawberry Reservoir begins in early June and extends through August; *O. tolmiei* begins a few weeks later and extends into September.

Twenty pairs of *C. linariifolia* and *A. tridentata* hosts were selected at each site. At Strawberry Reservoir an additional 20 pairs of *O. tolmiei* and *A. tridentata* hosts were selected. In addition, 5 uninfected *A. tridentata* were selected at both sites as hemiparasite-free controls.

Gas Exchange

Photosynthesis and stomatal conductance were measured with a portable gas-exchange system (LI-6200, Licor Instruments, Lincoln, NE, USA) twice during the *C. linariifolia* growing season at the Tintic and Strawberry Reservoir sites. Specific dates were chosen to correspond with the early and late parts of the parasite growing season. At both sites data were collected during diurnal peak photosynthesis (1000–1300 h MST) on 20 pairs of *C. linariifolia* and infected *A. tridentata,* and on an additional 5 uninfected *A. tridentata.* During the late season at Strawberry Reservoir, measurements were taken on an additional 20 pairs of *O. tolmiei* and infected *A. tridentata.* After gas-exchange measurements were completed, foliage was removed for leaf-area measurements using a leaf-area meter (LI-3100, Licor Instruments, Lincoln, NE, USA).

Water Potentials

Stems of approximately equal length and diameter were selected for predawn water-potential (Ψ_{pd}) measurements using a pressure bomb (PMS Instruments, Corvallis, OR, USA) for 20 infected and 5 uninfected *A. tridentata* at both sites. These measurements were taken approximately every 2 wk from May through early July at the Tintic site and late June through the end of August at the Strawberry Reservoir site.

Carbon Isotope Composition

Carbon isotope ratios ($\delta^{13}C$) were analyzed for the same plants used to measure gas exchange. The foliage was dried for 24 h and then finely ground with a mortar and pestle to homogenize the tissue (Ehleringer and Osmond 1989). Subsamples of 1–2 mg were combusted to produce CO_2, which was measured using an isotope ratio mass spectrometer (delta-S, Finnigan MAT, Bremen, Germany). Results are expressed using the $\delta^{13}C$ notation (‰), which relates the isotopic composition of the sample to the PDB standard as follows:

$$\delta^{13}C = \left[\frac{R_{sample}}{R_{standard}} - 1 \right] * 1000‰, \qquad (1)$$

where R represents the ratio of $^{13}CO_2/^{12}CO_2$ of the sample and standard, respectively (Ehleringer and Osmond 1989). All isotope ratio analyses were conducted at the Stable Isotope Ratio Facility for Environmental Research at the University of Utah, Salt Lake City, Utah, USA.

Calculation of Heterotrophy

Heterotrophy was calculated using measured and predicted $\delta^{13}C$ ratios. The predicted $\delta^{13}C$ ratio (δ_{pp}), the carbon isotope composition of a leaf provided that all carbon is autotrophic, was estimated with intercellular CO_2 concentrations (c_i) from gas-exchange measurements. Equation 2 relates c_i to the leaf carbon isotope ratio as modeled by Farquhar et al. (1982):

$$\delta_p = \delta_a - a - (b - a)(c_i/c_a), \qquad (2)$$

where δ_p is the $\delta^{13}C$ of the plant (= δ_{pp} in this study), δ_a is the approximate $\delta^{13}C$ of the air (−7.8‰), a and b are discrimination factors due to diffusion (4.4‰) and carboxylation via RuBP carboxylase (27‰), respectively. c_a is the concentration of CO_2 in air (ppm) and c_i was calculated from gas-exchange measurements described above. Heterotrophy (H) was calculated for the 1994 data (9 *C. linariifolia*, 5 infected and 5 uninfected *A. tridentata*) using Equation 3:

$$H = \frac{\delta_{pp} - \delta_m}{\delta_{pp} - \delta_h}, \qquad (3)$$

where δ_{pp} is the predicted $\delta^{13}C$ for the parasite, δ_m is the $\delta^{13}C$ measured in the parasite tissue, and δ_h is the $\delta^{13}C$ measured in the host tissue (Press et al. 1987a).

Statistical Analysis

Analysis of variance was used to compare yearly, seasonal, and plant means within a site for all photosynthetic data, and yearly and seasonal means for carbon isotope ratios (JMP, Version 3, SAS Institute Inc., Cary, NC, USA). The Tukey-Kramer Honestly Significant Difference test (HSD) was used to make specific comparisons. In addition, for each hemiparasite, carbon isotope ratios were compiled for all seasons and sites, and differences between hemiparasites and hosts were compared using a *t* test. A paired *t* test was used to determine differences between predicted and measured $\delta^{13}C$ for each *C. linariifolia*, uninfected and infected *A. tridentata*. Differences in Ψ_{pd} water potential between infected and uninfected *A. tridentata* were determined by *t* tests within each date.

RESULTS

Analysis of annual trends in photosynthetic rates for Strawberry Reservoir (Fig. 1) revealed that plants had significantly higher rates in 1995 than in 1994 for both parasite and host (Tukey-Kramer, $\alpha = 0.05$). For example, in 1995 photosynthetic rates for *C. linariifolia* and infected *A. tridentata* were 18.3 ± 2.1 and 16.0 ± 0.6 μmol m^{-2} s^{-1}, respectively, more than double those during the 1994 season. We also found seasonal differences in photosynthetic rates at Strawberry Reservoir. Both *C. linariifolia* and infected *A. tridentata* at Strawberry Reservoir experienced a significant decline in photosynthetic rates late in the season, with rates falling ~6.7 and 8.6 μmol m^{-2} s^{-1}, respectively (Tukey-Kramer, $\alpha = 0.05$). However,

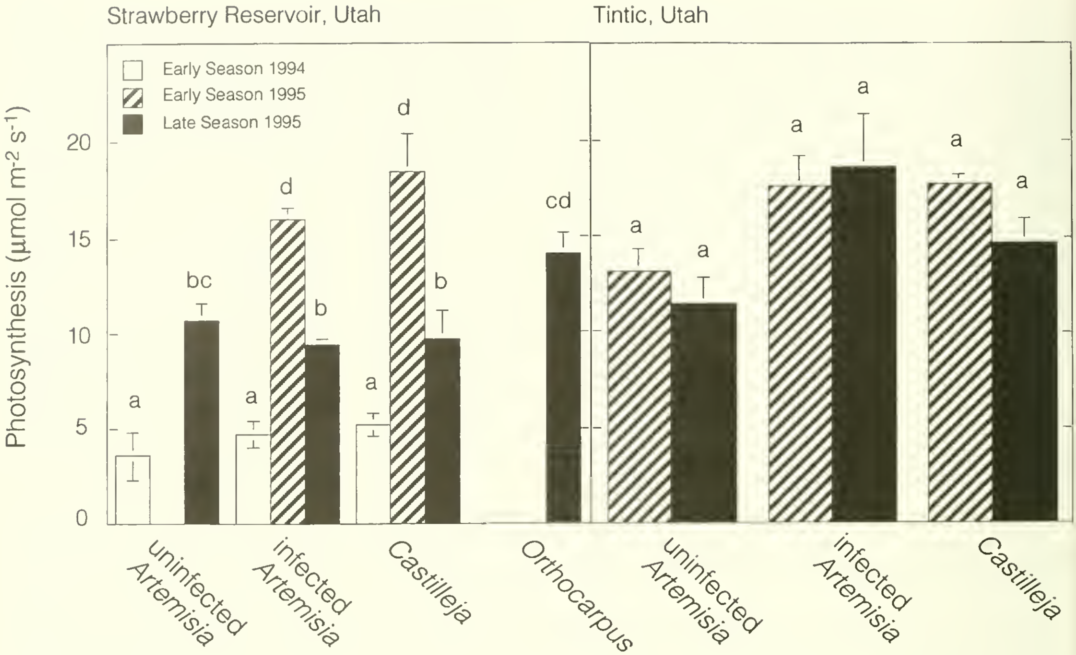

Fig. 1. Mean photosynthetic rates for hosts and parasites. Sites and sample sizes are as follows: Uninfected *A. tridentata* (Tintic: $n = 3$ for early season, $n = 4$ for late season; Strawberry Reservoir: $n = 3$ for late season), infected *A. tridentata* (Tintic: $n = 12$ for early season, $n = 7$ for late season; Strawberry Reservoir: $n = 7$ for early season, $n = 19$ for late season), *C. linariifolia* (Tintic: $n = 4$ for early season, $n = 6$ for late season; Strawberry Reservoir: $n = 3$ for early season, $n = 5$ for late season), *O. tolmiei* (Strawberry Reservoir: $n = 5$ for late season). Data are shown for Strawberry Reservoir (left panel) and Tintic (right panel) during the 1994 early season (open bars), 1995 early season (hatched bars), and 1995 late season (solid bars). Letters denote significant differences within each site. Error bars represent ± 1 $s_{\bar{x}}$.

photosynthetic rates at Tintic showed no seasonal differences (ANOVA, $F = 1.88$, $P = 0.134$; Fig. 1). In spite of annual and seasonal differences in photosynthesis for parasite and host plants, we found no difference in photosynthetic rates between *C. linariifolia* and infected *A. tridentata*. In contrast, *O. tolmiei* rates (14.0 ± 1.1 μmol m^{-2} s^{-1}) exceeded those for infected *A. tridentata* (9.3 ± 0.4 μmol m^{-2} s^{-1}; Tukey-Kramer, $\alpha = 0.05$; Fig.1).

At both sites we found no significant difference in predawn water potentials (Ψ_{pd}) between infected and uninfected *A. tridentata* ($P > 0.05$ for all dates, t test), although there was a general decline throughout the season (Fig. 2). The range in Ψ_{pd} was similar between sites; however, the values were slightly more negative at Tintic.

Carbon isotope ratios differed between years for infected and uninfected *A. tridentata*, with more negative values in 1995. However, $\delta^{13}C$ values for *C. linariifolia* did not differ between years (Tukey-Kramer, $\alpha = 0.05$; Table 1). Our results showed a slight seasonal decline in $\delta^{13}C$ values for parasites and hosts at Strawberry Reservoir, although only *O. tolmiei* and infected *A. tridentata* were significantly different (Tukey-Kramer, $\alpha = 0.05$; Table 1). This trend in seasonal reduction was not evident for plants at the Tintic site. Furthermore, we found that hemiparasite $\delta^{13}C$ ratios were significantly more negative than those of the hosts (*C. linariifolia*, $t = 12.57$, $P < 0.001$; *O. tolmiei*, $t = 11.94$, $P < 0.001$). In 1994 *C. linariifolia* $\delta^{13}C$ values (–28.9 ± 0.34‰) were nearly 3‰ more negative than those of the hosts (–26.2 ± 0.13‰), while this difference narrowed in 1995 to ~2‰ at Tintic and ~1.5‰ at Strawberry Reservoir.

Results from experiments in 1994 showed a significant mean difference of 1.34‰ between predicted and measured $\delta^{13}C$ ratios for *C. linariifolia* (paired t test, $t = 2.745$, $P < 0.05$; Table 2). Using this difference we calculated that, on average, 40% of *C. linariifolia* leaf carbon was host derived; individual plants ranged from 16 to 60% (Table 3). *C. linariifolia* heterotrophy is well within the range of values calculated for obligate hemiparasites. There was no statistical difference between measured and predicted $\delta^{13}C$ values for either infected or

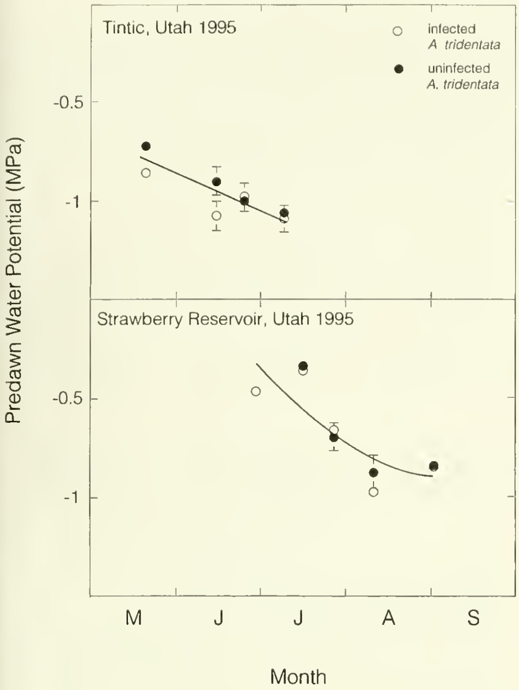

Fig. 2. Seasonal course of predawn water potentials for infected *A. tridentata* (open circles; $n = 11$) and uninfected *A. tridentata* (solid circles; $n = 5$). Data are provided for Tintic (upper panel) and Strawberry Reservoir (lower panel) from May to late August of 1995. Error bars represent ± 1 $s_{\bar{x}}$.

uninfected *A. tridentata*, indicating no heterotrophic carbon gain as expected.

DISCUSSION

Our results suggest that, with the exception of photosynthesis, the hemiparasites in this study behaved similarly to other hemiparasites. Photosynthetic rates for hemiparasites in this study were higher than rates for most other hemiparasites and similar to those of their autotrophic host plants. We also found large differences between years, which likely reflected differences in precipitation. In agreement with other studies, hemiparasite $\delta^{13}C$ ratios were more negative than those of the host (Press et al. 1987a, Marshall and Ehleringer 1990, Schulze et al. 1991, Richter et al. 1995). Furthermore, large differences in $\delta^{13}C$ ratios between the parasite and host suggested that the hemiparasite utilized a substantial amount of host-derived carbon. Despite relatively high photosynthetic rates, heterotrophy estimates for *C. linariifolia* range from 16% to 69%.

We found large interannual differences in photosynthetic rates and carbon isotope ratios for *C. linariifolia* and *A. tridentata*, which most likely indicated a response to precipitation differences. Climate records showed that the growing season at Strawberry Reservoir in 1994 was considerably drier than in 1995; the spring (March–May) of 1994 received only 96.3 mm of precipitation, whereas precipitation in the spring of 1995 totaled 216.4 mm (Utah Climate Center, Heber station). Differences in precipitation during the spring influence the amount of soil water available to the plants. This water supply can be indirectly assessed by measuring the plant's water potential before the sun rises and photosynthesis commences. Our Ψ_{pd} measurements corroborated that 1994 was a drier growing season; during 1994 the Ψ_{pd} range for *A. tridentata* (–1.7 to –3.2 MPa) was much more negative than the Ψ_{pd} range for *A. tridentata* in 1995 at either Tintic (–0.7 to –1.1 MPa) or Strawberry Reservoir (–0.3 to –0.9 MPa). Photosynthetic rates doubled during 1995, presumably in response to this increased precipitation. Interannual differences were most pronounced for *C. linariifolia*, which showed photosynthetic rates 3-fold higher in 1995 relative to rates in 1994. Carbon isotope ratios for autotrophic C_3 plants represent an estimate of long-term water-use efficiency (mmol C/mol H_2O; WUE), with more negative $\delta^{13}C$ ratios reflecting a lower WUE (Ehleringer and Osmond 1989). $\delta^{13}C$ ratios for infected and uninfected *A. tridentata* were significantly more negative during the wetter year, thus suggesting they were less conservative in their water use. Using $\delta^{13}C$ ratios as a measure of water-use efficiency is inappropriate for hemiparasites because of the potentially confounding effects of assimilating heterotrophic carbon. Therefore, it follows that the $\delta^{13}C$ ratio for *C. linariifolia* should also reflect influences from the import of host-derived carbon rather than simply the influences of increased precipitation. This prediction was supported by *C. linariifolia* data, where, despite the large increase in precipitation, we saw no difference in $\delta^{13}C$ ratios between years.

Photosynthetic rates also responded to seasonal influences, although rates were not different between parasites and hosts. Photosynthetic rates declined during the growing season, which, in part, may be attributed to the drier conditions late in the season as indicated

TABLE 1. Carbon isotope ratios ($\delta^{13}C$) for hosts and parasites. Sites and sample sizes are as follows: Uninfected *A. tridentata* (Strawberry Reservoir 1994: $n = 5$; Strawberry Reservoir 1995: $n = 3$ for early season; Tintic 1995: $n = 4$ for early season, $n = 5$ for late season), infected *A. tridentata* (Strawberry Reservoir 1994: $n = 5$; Strawberry Reservoir 1995: $n = 20$ for early season, $n = 30$ for late season; Tintic 1995: $n = 10$ for early season, $n = 11$ for late season), *C. linariifolia* (Strawberry Reservoir 1994: $n = 9$; Strawberry Reservoir 1995: $n = 7$ for early season, $n = 8$ for late season; Tintic 1995: $n = 11$ for early season, $n = 8$ for late season), and *O. tolmiei* (Strawberry Reservoir 1995: $n = 9$ for early season, $n = 19$ for late season). Letters denote significant seasonal differences within a site and species (Tukey-Kramer HSD, $\alpha = 0.05$). Values shown are means ± 1 $s_{\bar{x}}$. NA denotes data not available.

		A. tridentata			
Site	Year	Uninfected	Infected	*C. linariifolia*	*O. tolmiei*
Strawberry Reservoir	1994	-25.56 ± 0.32^a	-26.24 ± 0.13^a	-28.93 ± 0.34^a	NA
	1995				
	Early	-27.86 ± 0.1^b	-27.30 ± 0.11^b	-28.91 ± 0.15^a	-28.66 ± 0.09^a
	Late	NA	-27.80 ± 0.09^c	-29.33 ± 0.25^a	-29.50 ± 0.10^b
Tintic	1995				
	Early	-27.57 ± 0.19^b	-27.32 ± 0.21^{bc}	-29.19 ± 0.22^a	NA
	Late	-27.33 ± 0.19^b	-27.17 ± 0.16^b	-29.23 ± 0.15^a	NA

by predawn water potentials. Perhaps, the decline in *C. linariifolia* photosynthesis was also related to the phenology of the hemiparasite. It is possible that late in the season when these hemiparasites set fruit, they rely less on current photosynthesis and more on heterotrophic carbon gain. Most studies of hemiparasite-host gas-exchange dynamics found that hemiparasite photosynthesis was much lower than that of the host (Hollinger 1983, Press et al. 1987b, Pate et al. 1990, Marshall, Dawson, and Ehleringer 1994). *S. hermonthica* and *S. asiatica* have photosynthetic rates that are half of those for *Sorghum* hosts (Press et al. 1987b). In contrast, the photosynthetic activities of *C. linariifolia* in this study were similar to rates of *A. tridentata* hosts. This pattern remained stable from year to year, despite large differences in precipitation.

Hemiparasite gas-exchange rates have been used to make inferences about potential heterotrophic carbon use. After calculating that 8.8–18.9 h of light-saturated photosynthesis was necessary for 8 different species of facultative hemiparasites to reach zero net foliar carbon gain, Press et al. (1988) hypothesized that they must have had access to a heterotrophic carbon supply. Conversely, in *Bartsia trixago* and *Parentucellia viscosa* (Scrophulariaceae), where photosynthetic rates were very similar to autotrophic plants, it was predicted that these facultative root hemiparasites were less reliant on host-derived carbon (Press et al. 1993). Since *C. linariifolia* also has photosynthetic rates similar to those of its host, it follows that *C. linariifolia* might not contain significant amounts of heterotrophically derived carbon.

However, in our study this was not the case. We found a relatively large difference in $\delta^{13}C$ ratios between *C. linariifolia* and *A. tridentata* hosts, which likely indicates hemiparasite heterotrophy. Indeed, we calculated that *C. linariifolia* in this study utilized an average of 40% host-derived carbon. As with other parasitic plants, unusually high transpiration rates relative to the hosts represent the most likely driving force for this assimilation of host-derived carbon. While the estimates of heterotrophy found in this study are well within the range of those reported for other parasites, one must consider the inherent obstacles in using an instantaneous measure of photosynthesis as a basis for the predicted $\delta^{13}C$ ratios with an integrated measure of actual leaf $\delta^{13}C$ ratio. For instance, differences in gas-exchange characteristics at the time leaf carbon was incorporated may contribute to differences between predicted and measured $\delta^{13}C$ ratios. Although, we found no significant difference between predicted and measured $\delta^{13}C$ ratios for infected and uninfected *Artemisia*, a better control would have been autotrophic *C. linariifolia* plants if they had been available. As mentioned earlier, parasites may also access different pools of carbon at different times throughout the growing season; in turn, this may influence the $\delta^{13}C$ ratios measured in the leaf carbon. While these factors may appear troublesome at first, they represent a few of the many areas open to investigation in parasitic plant ecophysiology.

TABLE 2. Measured and predicted $\delta^{13}C$ values for uninfected and infected *A. tridentata* ($n = 5$) and *C. linariifolia* ($n = 9$) at Strawberry Reservoir in 1994. Means ± 1 $s_{\bar{x}}$ are presented. Also shown is the difference between the predicted and measured values. * denotes significant difference at $P < 0.05$ (paired t test).

	A. tridentata		
	Uninfected	Infected	*C. linariifolia*
$\delta^{13}C_{measured}$	−25.56 ± 0.32	−26.24 ± 0.13	−28.93 ± 0.34
$\delta^{13}C_{predicted}$	−26.54 ± 0.93	−25.11 ± 0.86	−30.26 ± 0.24
Difference	−0.98 ± 1.19	1.13 ± 0.94	−1.34 ± 0.48*

TABLE 3. Calculated heterotrophy of *C. linariifolia* in this study compared to heterotrophy calculated for other hemiparasites.

Species	Calculated heterotrophy in % (range)	Source
Castilleja linariifolia	40 (16–69)	This study
Striga hermonthica, *Striga asiatica*	28–35	Press et al. 1987, Graves et al. 1989
Phoredendron juniperinum	61	Marshall and Ehleringer 1990
Mistletoe species	60 (49–67)	Schulze et al. 1991
Australian mistletoe	15 (5–21)	Marshall et al. 1994b

Though no other study quantifies heterotrophic carbon gain by a facultative hemiparasite, a study by Hansen (1979) implied potential heterotrophy in *Castilleja chromosa*. Experiments measuring the difference of ^{14}C labeled sugar content in uninfected and infected *Artemisia tridentata* individuals showed less ^{14}C in the infected host tissues. Hansen (1979) hypothesized that this difference represented sugar lost to the *C. chromosa* parasite. With this indirect method, *C. chromosa* utilized, on average, 10% host-derived carbon. Using a more precise method, we would suggest from our study that 10% heterotrophy may be an underestimate.

Significant heterotrophic carbon gain by the hemiparasite can be associated with a decrease in host production. Graves et al. (1989) found that dry weight of *Sorghum* infected with *S. hermonthica* was 40% less than that of uninfected *Sorghum*, and hypothesized that the effects of *S. hermonthica* were due to (1) the direct reduction in host carbon by parasite heterotrophy and (2) the indirect reduction of host photosynthetic potential. Press and Stewart (1987) showed that photosynthetic rates for *Sorghum* infected by *S. hermonthica* were reduced by nearly half relative to those for uninfected *Sorghum*; stomatal conductance rates were also significantly decreased. In contrast, we saw no decrease in photosynthetic rates nor stomatal conductance rates for infected *A. tridentata*. Interestingly, there was an increase in host photosynthesis relative to uninfected *A. tridentata* late in the season at Tintic. Our study also showed no difference in Ψ_{pd} between infected and uninfected *A. tridentata*, suggesting that hosts in this study were not experiencing detectable water stress. Taken together these data seem to suggest that *C. linariifolia* do not negatively impact *A. tridentata* hosts. However, this conclusion may be relevant only during unusually wet years; *A. tridentata* may respond differently to hemiparasite infection when drought conditions prevail.

One well-supported aspect of the host-parasite relationship is the unusually high transpiration rates of the parasite, often 10 times greater than those of the host. It is generally believed that this high water flux results in a water potential gradient from the host to the parasite. Therefore, through this mechanism higher transpiration rates are thought to represent the driving force for the transfer of solutes from the host to parasite. Schulze et al. (1984) suggested that high transpiration rates may be necessary for mistletoe to acquire adequate nitrogen for growth. The nitrogen-gathering hypothesis has been the focus of several studies (Schulze et al. 1984, Ehleringer et al. 1985, Marshall, Dawson, and Ehleringer 1994). However, as Raven (1983) points out, these plants are also inextricably acquiring significant amounts of host carbon. Recent studies indicated that heterotrophy may be a widespread phenomenon occurring in a variety of obligate hemiparasites (Press et al. 1987a, Graves et al. 1989, Marshall and Ehleringer 1990, Marshall et al. 1994, Richter et al. 1995). Evidence from this study indicates that the facultative root parasite *C. linariifolia* obtains a substantial contribution of host-derived carbon, thus extending further emphasis to the importance of this carbon supply for hemiparasites.

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HABITAT AND SPATIAL RELATIONSHIPS OF NESTING SWAINSON'S HAWKS (*BUTEO SWAINSONI*) AND RED-TAILED HAWKS (*B. JAMAICENSIS*) IN NORTHERN UTAH

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ABSTRACT.—A total of 28 Swainson's Hawk (*Buteo swainsoni*) and 30 Red-tailed Hawk (*B. jamaicensis*) nests were found in Cache Valley, Utah, during the summers of 1992 and 1993. All nests were in trees, but only Red-tailed Hawks nested in dead trees (30%). In the intensive study area, nesting densities were 0.10 nests/km^2 for Swainson's Hawk and 0.08 nests/km^2 for Red-tailed Hawk. Nearest-neighbor nest distances were significantly shorter among Swainson's Hawks (1.74 km) than among Red-tailed Hawks (2.83 km). Congeneric nearest-neighbor distances were significantly shorter than conspecific distances for Red-tailed Hawks (1.59 vs. 2.83 km) but not for Swainson's Hawks (1.52 vs. 1.74 km). GIS analysis of habitat types was made for 2-km radii around nest sites. Cropland was the dominant land cover type at nest sites of both species and no significant difference was found between species. Swainson's Hawk nest sites contained significantly more pasture, whereas Red-tailed Hawk nest sites contained significantly more juniper, maple, and sagebrush. Only Red-tailed Hawk nests (n = 8; 27%) were found on the periphery of the valley at the base of foothills of the Cache Mountains. This preference resulted in a significantly higher elevation for Red-tailed Hawk nest sites. Swainson's Hawk nests occurred only on the valley floor on level terrain. Distance to the nearest paved road and building was very similar for both species, implying that little difference exists in tolerance levels for human activities. Overall, multivariate niche overlap for habitat was high (0.89), indicating a lack of habitat partitioning between these 2 *Buteos* in Cache Valley.

Key words: Swainson's Hawk, Red-tailed Hawk, Buteo, *nest sites, habitat, GIS.*

Relatively few studies have included a comparison of nest sites, habitat, or densities of Swainson's Hawks (*Buteo swainsoni*) and Red-tailed Hawks (*B. jamaicensis*). Rothfels and Lein (1983) and Bechard et al. (1990) examined nearest-neighbor distances of these 2 species in Alberta and Washington, respectively, and Bechard et al. (1990) also compared habitats. Janes (1985) examined habitats associated with sightings of these 2 *Buteos* in Oregon. Considering that these species are sympatric throughout much of their range in western North America, further information on their habitat use and nesting density in overlapping regions would be useful for understanding patterns of coexistence.

The present study is also important because the Swainson's Hawk is considered to be declining in Utah, Nevada, and Oregon, and its status is listed as a "species of special concern" in Utah, Nevada, Oregon, and Washington, and "threatened" in California (Harlow and Bloom 1989). Conversely, Red-tailed Hawks are considered to be increasing (Harlow and Bloom 1989) due to an increase in perching habitat, at the expense of Swainson's Hawks (Janes 1985, 1987). Therefore, a comparative approach to the nesting ecology of these 2 species is not only of ecological importance but has implications for the future conservation of Swainson's Hawks.

STUDY AREA AND METHODS

The study was conducted in the Cache Valley portion of Cache County in northern Utah (Fig. 1). The valley comprises cropland (alfalfa, hay, winter wheat, corn), pasture, grassland, marsh, sagebrush-grassland, barnyards/feedlots, residential areas, and commercial complexes. During the summers of 1992 and 1993, we conducted a vehicle survey of the entire valley by driving on primary and secondary (dirt) roads along the valley floor and lower benches. Searches did not extend into mountainous terrain.

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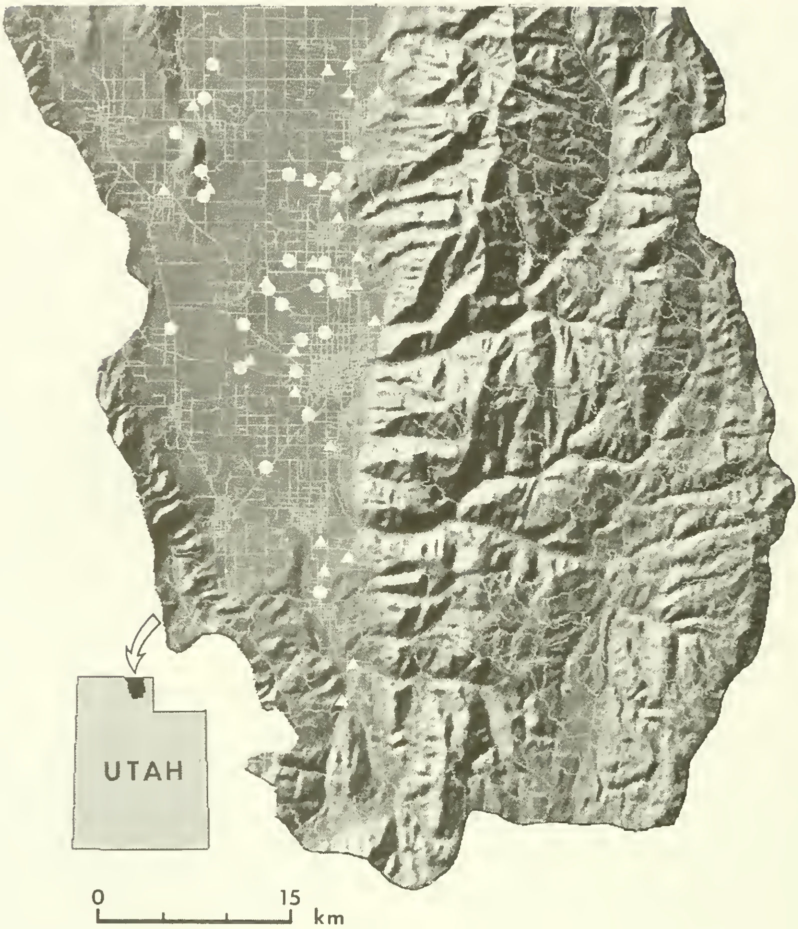

Fig. 1. GIS shaded relief map of the Cache Valley study area in northern Utah showing the distribution of Swainson's Hawk (circles) and Red-tailed Hawk (triangles) nests for 1992 and 1993 nesting seasons combined. Light lines indicate primary and secondary roads.

Occupied nests were found by scanning likely trees, especially if adults were seen nearby or protested our approach. A nest was considered occupied only if an incubating or brooding female and/or young were present. Nests were not examined for the presence of eggs. Because of the low density of trees (<1/ha) in the valley, we found nests relatively easily and could effectively search large areas by vehicle surveys. Although there were undoubtedly some nests that were missed in the valley, we felt there was a similar probability of detecting either species on all surveys, so comparisons should not be biased. Locations of all nests were plotted onto 7.5-min USGS topographic maps (1:24,000 scale quadrangles). Elevations of nest sites were obtained from the topographic maps. Slope was not calculated since the vast majority of nest sites occurred on level ground.

To examine nesting density, we completely searched an intensive study block (100 km^2) for nests during a single breeding season (1992) using the methods of Craighead and Craighead (1956). Since the intensive study area was completely flat and relatively treeless, spotting all territorial birds and nests in trees was not difficult. In the intensive study area, nest searching occurred from April through July, and all territorial birds were accounted for with occupied nests. This fact, combined with a lack of rocky outcrops and cliffs, assured us that there were no ground-nesting birds in the intensive study area. Nesting density was calculated as the absolute density of nests per total area of the intensive study block. Nearest-neighbor distances were calculated according to the method of Clark and Evans (1954).

Land-use/land-cover maps of Cache Valley were generated and field-checked from aerial photographs by Utah Division of Water Resources (1991). These maps were subsequently digitized into a vector-based (ARC/INFO) geographic information system (GIS) and were used as a base layer to determine habitats of the 2 *Buteos* in Cache Valley. Nest site locations on USGS quadrangles were subsequently digitized into the GIS. Habitat areas were calculated within a 2-km (1.2-mile) radius of nest sites. This represented a circular area of 1257 ha, which was about midway between the mean home range size reported for Swainson's Hawk (Fitzner 1980) and Red-tailed Hawk (U.S. Department of Interior 1979). Because some hawks built a new nest in the same territory the following year (1993), only 1 occupied nest per territory over the 2-yr period was used in the habitat analysis to avoid pseudoreplication. Distances to the nearest paved road and buildings were measured by pacing (<200 m) or using a vehicle odometer (>200 m). Habitats were classified by the Utah Division of Water Resources (1991) into 11 major habitat types: cropland, fallow field, grassland, pasture, sagebrush, juniper (*Juniperus* spp.), maple (*Acer grandidentatum*), riparian (wetlands, temporary marshes, mud flats), open water, residential, and commercial (non-residential buildings, industrial structures, junkyards, and parking lots).

Statistical analysis was performed on NCSS software (Number Cruncher Statistical Software, Kaysville, UT). Prior to analysis, habitat variables were tested for normality (D'Agostino 1990). A number of data transformations were attempted (Zar 1984), but none were able to normalize all variables. Therefore, a non-parametric rank test (Mann-Whitney *U*-test, 2-tailed) was selected for all habitat comparisons. To calculate habitat overlap from the GIS data variables, a full-model (all variables included) discriminant function analysis (DFA) was run to determine the extent of habitat partitioning between the 2 species. Multivariate niche overlap for habitat was calculated with log-transformed variables with the following formula presented by Maurer (1982):

$$\text{overlap} = \exp(-d^2/S1 + S2);$$

where d = the difference between mean discriminant scores for species 1 and 2, and S = the standard deviation of the discriminant scores. Maurer (1982) and Klopfer and Ganzhorn (1985) suggested that stepwise procedures that eliminate variables always result in a biased underestimation of niche overlap. Therefore, we used a full-model DFA instead of stepwise DFA because it considers the whole spectrum of habitat variables available for partitioning.

RESULTS AND DISCUSSION

We located 58 occupied nest sites during 1992 and 1993 field seasons: 28 Swainson's Hawk nests and 30 Red-tailed Hawk nests. In a single breeding season (1992), a maximum of 22 occupied nests were found for Swainson's Hawks and 23 for Red-tailed Hawks. All nests were in trees, although a few cliff sites were available in the study area but not occupied. Only Red-tailed Hawks nested in dead trees (9 of 30 trees), which was statistically significant because Swainson's Hawks nested only in live trees (Fisher Exact Test, 2-tailed, $P = 0.002$). Red-tailed Hawks nested higher aboveground and in taller trees, but tree diameter was not significantly larger (Table 1).

The intensive study area was completely searched for occupied nests in 1992 and contained 10 Swainson's Hawk nests and 8 Red-tailed Hawk nests (Fig. 2). Absolute nesting density in this area was 0.10 nests/km^2 for Swainson's Hawks and 0.08 nests/km^2 for Red-tailed Hawks. Gilmer and Stewart (1984) reported a nesting density of 0.055 nest/km^2 for Swainson's Hawk, which was almost half the density found in Cache Valley. Luttich et al. (1971) reported a nesting density of 0.145 red-tailed nests/km^2, which is higher than our study area. Rothfels and Lein (1983) reported nesting densities of 0.238 nests/km^2 for Swainson's and 0.508 nests/km^2 for Red-tailed Hawks, which were much greater than the density for Swainson's and Red-tailed Hawks in Cache Valley. This difference probably reflects the fact that hawk nests can be dispersed because of areas of unsuitable and marginal habitat (e.g., note that nests were not located within areas of dense suburban road networks in Fig. 2).

Newton (1979) stated that in continuously suitable habitat the nests of the same species are often separated by roughly equal distances. Mean nearest-neighbor distance (Clark and Evans 1954) is the measure that can be used to

TABLE 1. Nest tree and topographic variables of Swainson's and Red-tailed Hawk nest sites in northern Utah. Data represent means ± s with sample size in parentheses.

	Red-tailed Hawk	Swainson's Hawk	P^a
Nest tree height (m)	17.3 ± 4.1 (25)	13.9 ± 2.9 (23)	0.001
Nest height (m)	14.8 ± 3.4 (23)	11.3 ± 3.3 (21)	0.002
Nest tree DBH (cm)	87.2 ± 39.4 (22)	75.5 ± 44.6 (23)	0.226
Distance to paved road (m)	393.6 ± 580.9 (30)	311.6 ± 484.2(23)	0.133
Distance to building (m)	246.1 ± 174.3 (30)	250.4 ± 174.2(24)	0.649
Elevation (m)	1401 ± 193.6 (29)	1373 ± 31.4 (27)	0.001

[a]Mann-Whitney U-test, 2-tailed

quantify these spacing patterns. In Cache Valley we found a significant difference (Student's t test, $t = 2.61$, $P < 0.02$) for this distance, which was 1.74 km for Swainson's Hawks ($n = 10$) and 2.83 km for Red-tailed Hawks ($n = 8$). In Alberta, Rothfels and Lein (1983) reported mean nearest-neighbor distances of 1.46 km for Swainson's Hawks and 0.88 km for Red-tailed Hawks. These results are similar to Swainson's Hawks in Cache Valley but are much shorter than our estimate for Red-tailed Hawks. Rothfels and Lein (1983) noted that their data on Red-tailed Hawks showed a much denser population than normal. The mean for 7 other Red-tailed Hawk studies was 1.95 km (data from Rothfels and Lein 1983), which is closer to the distance found for Cache Valley. The mean for 5 other Swainson's Hawk studies is 1.78 km (data from Rothfels and Lein 1983), very close to the mean for Cache Valley. Overall, nearest-neighbor distances from our study area were consistent with the majority of literature values, demonstrating the regular dispersion of nest sites that results from territorial behavior (Newton 1979).

Congeneric nearest-neighbor distances were significantly shorter than conspecific distances for Red-tailed Hawks (1.59 km vs. 2.83 km) but not for Swainson's Hawks (1.52 km vs. 1.74 km; Student's t test, $t = 2.18$, $P = 0.047$ and $t = 0.78$, $P = 0.44$, respectively). These results suggest that Red-tailed Hawks are more tolerant of close nesting by Swainson's Hawks than their own species, but Swainson's Hawks are equally intolerant to congeners and conspecifics. In Alberta, Schmutz (1977) and Rothfels and Lein (1983) found that congeneric *Buteos* nested closer together than conspecifics probably because competition among congenerics was less than among conspecifics.

With regard to distribution in the study area, only Red-tailed Hawks (27%; $n = 8$) nested above the valley floor at the base of foothills of the Cache Mountains (Fig. 1), and this difference resulted in a statistically significant increase in elevation (Table 1). Swainson's Hawks did not nest in this zone at all, possibly because many of these sites were already occupied by earlier-nesting Red-tailed Hawks or because of habitat preferences discussed below. Rothfels and Lein (1983) noted qualitatively that Swainson's Hawks usually nested on flatter terrain than Red-tailed Hawks. In this study, Swainson's and Red-tailed Hawk nests lacked a significant difference for the distance to nearest buildings or paved roads (Table 1). No previous studies of these 2 species have been conducted in areas with this much urbanization. Our data suggest that no significant differences exist in regard to tolerance of human activities and structures.

Overall, the GIS indicated that habitat around nest areas was dominated by cropland and pasture for both *Buteos* (Fig. 3). Swainson's Hawk nest sites had significantly more pasture (22.4% vs. 12.3%) but not cropland, fallow field, or grassland. In eastern Washington, Bechard et al. (1990) noted that Swainson's Hawks utilized wheatland and grassland more than Red-tailed Hawks. In this study Red-tailed Hawks nested in areas with significantly more tree cover (maple and juniper) and sagebrush, which predominated uplands along the edge of the valley floor. The importance of trees to Red-tailed Hawks was noted by Houston and Bechard (1983), who documented the increase in nesting by this species after the expansion of trees into the prairie regions of Saskatchewan. Similarly, Knight et al. (1982) found that Red-tailed Hawks nested exclusively in riverine forest land along the Columbia River, even though suitable cliff nesting areas were available. Janes (1985) noted that Swainson's Hawks depended more on aerial foraging and occurred in habitats containing few or no perches. In this study Red-tailed Hawks probably nested more in tree habitats because of greater perch availability/

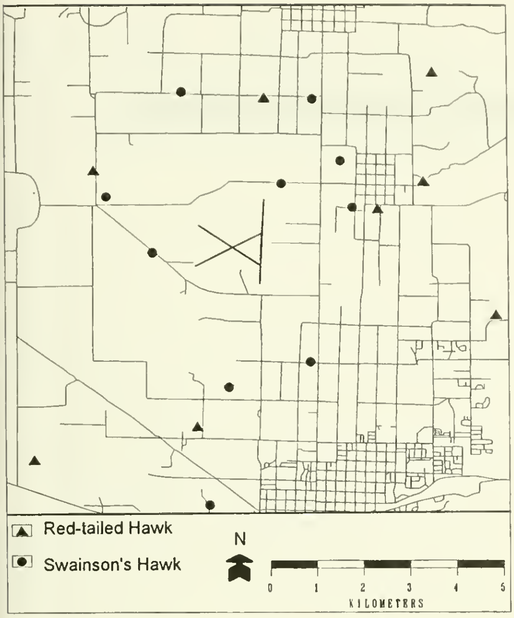

Fig. 2. GIS road map of 100-km^2 intensive study area centered at Logan Municipal Airport showing nest site locations for Swainson's and Red-tailed Hawks during the 1992 breeding season.

use, although other factors such as larger prey species may also be a factor.

Connell (1980) explained that resource partitioning (or low overlap) is due to the "ghost of competition past" (past competition), which has created evolutionary changes in morphology and behavior to avoid current competition. Since raptors are at the top of the food pyramid and occur at extremely low breeding densities (Newton 1979, Scheoner 1984), resources are likely to be limiting, and high overlap in resources between species is likely to result in current competition (except in rare cases such as vole plagues). Despite some significant differences for 4 of the 12 habitat types, we calculated a multivariate (DFA) niche overlap of 0.89 for habitat. Niche theory suggests that overlap values higher than 0.6 are needed to cause interspecific competition, while lower values indicate underutilization of the resource continuum resulting in intense intraspecific competition (see reviews by Bosakowski et al. 1992, Bosakowski and Smith 1992).

Prey overlap data were not collected in our study area, but Smith and Murphy's (1973) data from northern Utah showed a high prey overlap value of 0.80 for Red-tailed and Swainson's Hawks (as calculated by Jaksic 1983). In Montana, Restani (1991) found an even higher food overlap (0.93) for these 2 *Buteos*. Considering the findings of high overlap for food (Jaksic 1983, Restani 1991) and habitat (this study), competition between these *Buteos* should be expected whenever the species occur in close proximity. As further evidence, Schmutz et al. (1980) found that reproductive performance was significantly reduced in cases where these *Buteos* nested at close range.

Due to man-made alterations, few of the native plant communities presently exist in Cache Valley. Not surprisingly, we did not observe significant habitat partitioning between these 2 *Buteos* for the existing habitat types. Elsewhere, investigators have claimed that significant habitat partitioning (non-overlap) occurred between these *Buteos* in Oregon (Janes 1985) and Washington (Bechard et al. 1990), but the extent of habitat overlap was not previously quantified. Our results indicate that statistical tests can show differences among several habitat variables, while the overlap value can still remain critically high.

Competition for habitat has also been demonstrated by behavioral observations of Swainson's Hawks frequently usurping portions of Red-tailed Hawk territories with lower perch densities (Janes 1994). Alternately, Janes (1985, 1987) noted that the increase in perching habitat, caused by the spread of junipers, homesteads, and utility poles, "favors the Red-tailed Hawk at the expense of the Swainson's Hawk." In addition, Janes (1994) also reported that territorial Swainson's Hawks are occasionally displaced by Red-tailed Hawks.

Bednarz (1988) noted that availability of nest trees could be a limiting factor for Swainson's Hawks because of their affinity for open grassland and desert habitats that are often devoid of trees. Similarly, Houston and Bechard (1983) reported the expansion of Red-tailed Hawks in Saskatchewan following the spread of trees into prairie regions. In our study area the western portions of the valley floor were often treeless and usually supported little nesting for either species (note lower density of nests in Fig. 1). For such situations Schmutz et al. (1984) recommended installation of artificial nest platforms for Swainson's Hawks, which significantly increased nesting density in his experiments. However, if artificial nest platforms are used, we recommend caution and close monitoring so as not to give advantage to the more

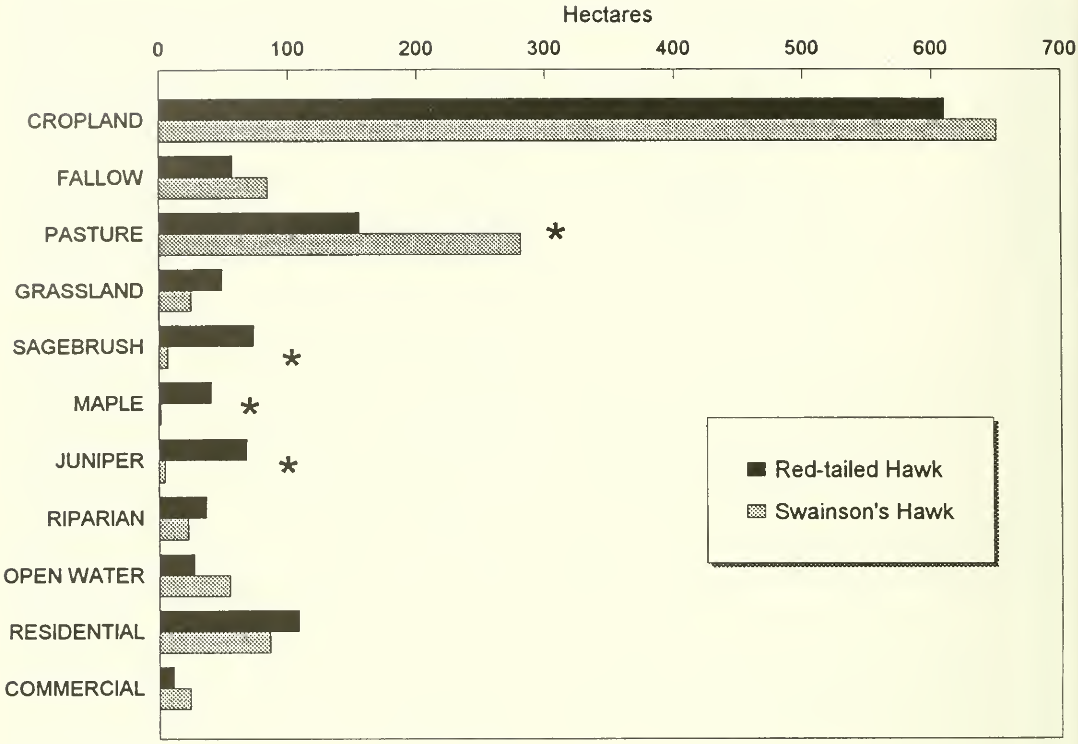

Fig. 3. Habitat areas around nest sites (2 km radius) of Swainson's ($n = 26$) and Red-tailed Hawks ($n = 28$) from Cache Valley, Utah, as determined from GIS analysis. Bars represent the mean and stars indicate that a significant difference was observed between species (Mann-Whitney *U*-test, 2-tailed, $P < 0.05$).

common Red-tailed Hawks. In our study area only Red-tailed Hawks nested in snags (30% of occupied nests) and may be more likely to use an open-topped artificial platform than Swainson's Hawks, which always nested in green trees. Many of the snags used by Red-tailed Hawks in Cache Valley were caused by failure to irrigate croplands during recent drought conditions, thus changing the suitability of nest sites in favor of Red-tailed Hawks.

In the future close attention to irrigation and surveillance of land-use changes are likely to be the most important factors in conserving Swainson's Hawks in Cache Valley. Economic conversion of agrarian land use to commercial and residential real estate is currently in progress, and impacts to future Swainson's Hawk populations need to be carefully monitored. Due to the rapid human population growth in Cache Valley, we recommend annual monitoring for Swainson's Hawk territories and nests, which may be impacted by future development or land-use changes. This monitoring management will require frequent updating of the GIS database to track habitat changes in the future so that necessary mitigation steps can be evaluated.

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WESTERN BALSAM BARK BEETLE, *DRYOCOETES CONFUSUS* SWAINE, FLIGHT PERIODICITY IN NORTHERN UTAH

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ABSTRACT.—The flight periodicity of western balsam bark beetle (*Dryocoetes confusus* Swaine) in Big Cottonwood Canyon, Utah, was studied during the summer months of 1992, 1993, and 1994. Contents of baited funnel traps were tallied by species up to 3 times weekly. Two main periods of flight activity were observed each year. The first and, generally, largest occurred in early summer soon after flight was initiated for the season. A 2nd period was observed in late summer, generally August. Timing of the 2 periods was influenced by unusually warm or cool weather in each study year. The 1st period had more males than females while the 2nd period had a majority of females. Except during periods of cool or wet weather, western balsam bark beetles were found to be active at least at minimal levels from June through September.

Key words: Dryocoetes confusus, *flight periodicity, Scolytidae, insect control, insect phenology,* Abies lasiocarpa, *Utah forests.*

The western balsam bark beetle, *Dryocoetes confusus* Swaine (Coleoptera: Scolytidae), is a serious insect pest of true firs. This insect's life cycle is not fully understood (Johnson 1985), however, possibly due to the traditionally low commercial value of its host. In British Columbia, for example, timber losses from western balsam bark beetles have only relatively recently been calculated (Doidge 1981). The need to understand the life cycle and behavior of this bark beetle has increased in relation to the increased commercial and aesthetic value of true firs.

Drought-subjected subalpine fir, *Abies lasiocarpa* (Hook.) Nutt., in northern Utah has been experiencing a western balsam bark beetle outbreak that began in 1989. Most of the affected trees are on the heavily visited Wasatch-Cache National Forest, including the canyons east of Salt Lake City where picnic areas, campgrounds, and ski resorts are common. This caused local forest managers to seek beetle abatement measures. Bark beetle control strategies, such as deployment of semiochemicals or cultural treatments, require knowledge of the time frame in which beetles emerge from infested host material to attack new hosts. This is a report of 3 yr of western balsam bark beetle flight periodicity data from Big Cottonwood Canyon, Utah. Sex ratios, weather influences, and associated scolytids are also presented.

MATERIALS AND METHODS

Five plots were established on 5–6 June 1992 in Big Cottonwood Canyon, Utah, ranging from 2000 to 2840 m elevation. Plots were selected from areas of recent beetle activity indicated by fading or red subalpine fir crowns.

The plot at 2000 m has a white fir (*Abies concolor* [Gord and Glend.] Lindl. ex Hildebr.)/ Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco) mix and also had the least amount of fading host material of any plot. This is generally the lower elevational band for subalpine fir in Big Cottonwood Canyon. Small amounts of subalpine fir can be found immediately uphill from the plot. The higher plots are dominated by subalpine fir, sometimes in association with Douglas-fir, quaking aspen (*Populus tremuloides* Michx.), or Engelmann spruce (*Picea engelmannii* Parry ex Engelm.).

Each plot contained three 16-unit Lindgren funnel traps[2] spaced at about 50-m intervals in a triangular pattern. Traps were baited with a semiochemical mixture containing *exo*-brevicomin (racemic) released at 1 mg/24 h at 24°C[3] (Borden et al. 1987). Traps were hung as high as possible on branches, leaving the trap cup about 1.5 m aboveground. Trap cups were emptied up to 3 times weekly to reduce losses to predation. Cups were emptied less frequently late in each study year as captures diminished. Western balsam bark beetles were tallied along with associated scolytids and important predators, namely checkered beetles (*Enoclerus* spp.). Identification of associated scolytids was provided by Stephen L. Wood[4]. *D. confusus* captures for the entire season were then totaled for each plot. The percentage of the annual total caught at each observation was then plotted against date for each location.

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The study was repeated starting in mid-May 1993 with 5 plots installed from 1750 to 2840 m elevation. Two sites from 1992 were reused, 2 were moved a short distance (about 100 m horizontal), and 1 was new. The lowest elevation plot was deliberately established in the white fir zone. Low-elevation plots were installed earlier in the year than in 1992 to ensure placement before beetle flight commenced. Plots at 1750 and 2350 m were installed 25 May 1993, and the plot at 2560 m was established 27 May 1993. The plot at 2660 m was installed on 8 June 1993 and the plot at 2840 m on 21 June 1993.

The 1994 flight periodicity study utilized the 4 highest sites from 1992, ranging in elevation from 2310 to 2840 m. These areas continued to contain fading host material throughout each study year. The low-elevation sites, lacking a substantial subalpine fir component, were dropped from the study due to the small populations of *D. confusus* in those areas. The plot at 2310 m was established on 10 May 1994, while the remaining plots were installed on 25 May 1994. This gives 3 consecutive years of flight period data for 4 locations.

The first 10 *D. confusus* from each trap cup observation, totaling 30 per plot, were tallied for sex in 1993 and 1994. Females were identified by a prominent setal brush on the frons (Borden et al. 1987). For 1993 and 1994 the sex ratio of each distinct flight surge was compared. The division between surges was determined from each significant flight activity lapse not associated with cool or wet weather.

Weather data from Brighton–Silver Lake[5] was compared with flight activity for the plots at 2600/2660 m and 2840 m (this station is geographically and elevationally between the 2 plots). Daily maximum/minimum temperatures and daily precipitation were plotted from 20 May through 31 October for each study year.

RESULTS

Flight Periodicity

1750 METERS.—This site was used only in 1993 with a total of 42 *D. confusus* captures. Consequently, I deleted it from consideration for the purpose of this study. Nearby white fir mortality that was examined contained evidence only of fir engraver beetle, *Scolytus ventralis* LeConte.

2000 METERS.—Because this site had relatively few captures, I used it only in 1992. Flight activity for that year sharply peaked in mid- to late June (Fig. 1). A substantially smaller surge occurred in early August. *D. confusus* captures totaled 1469. The 1st wave of activity accounted for 84% of total captures.

2310/2350 METERS.—The substantial number of captures at the first observation of 8 June 1992 indicates that flight was likely initiated before plot establishment (Fig. 2). Captures peaked in mid-June with activity continuing throughout the month. A 2nd surge began in mid-July and tapered off in mid-August. *D. confusus* captures totaled 19,071. Forty-one percent of the total occurred in the 1st surge.

In 1993 traps at this plot began to capture beetles in mid-June with a small peak occurring in late June. A 2nd wave of captures began in late July, peaking in mid- to late August. *D. confusus* captures were about 9% of those in 1992, totaling 1800. The 1st wave of captures accounted for 10% of the total.

Capture patterns of 1994 were very similar to those of 1992. The first positive observation was on 3 June 1994. An early summer peak occurred on 13 June 1994 with activity tapering off in late June through early July. A late-summer surge occurred in mid- to late July with captures gradually diminishing through early October. *D. confusus* captures totaled 2574, with 30% caught in the 1st surge.

2560 METERS.—The first 1992 observation was positive, indicating that flight was possibly initiated before plot establishment. Beetles

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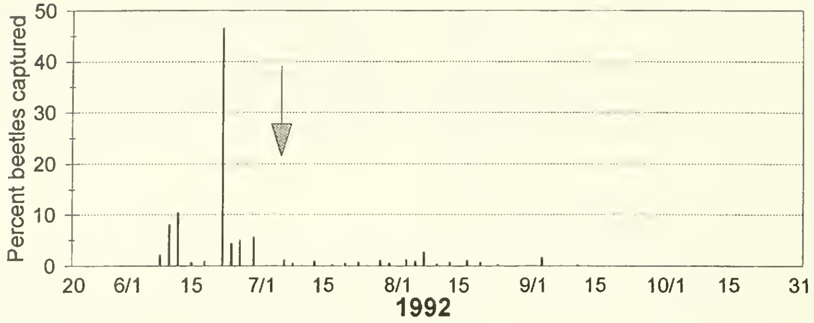

Fig. 1. Percentage of total (n = 1469) seasonal *Dryocoetes confusus* captures per observation at 2000 m, 20 May–31 October. Arrow indicates the trough between surges not associated with cool or wet weather.

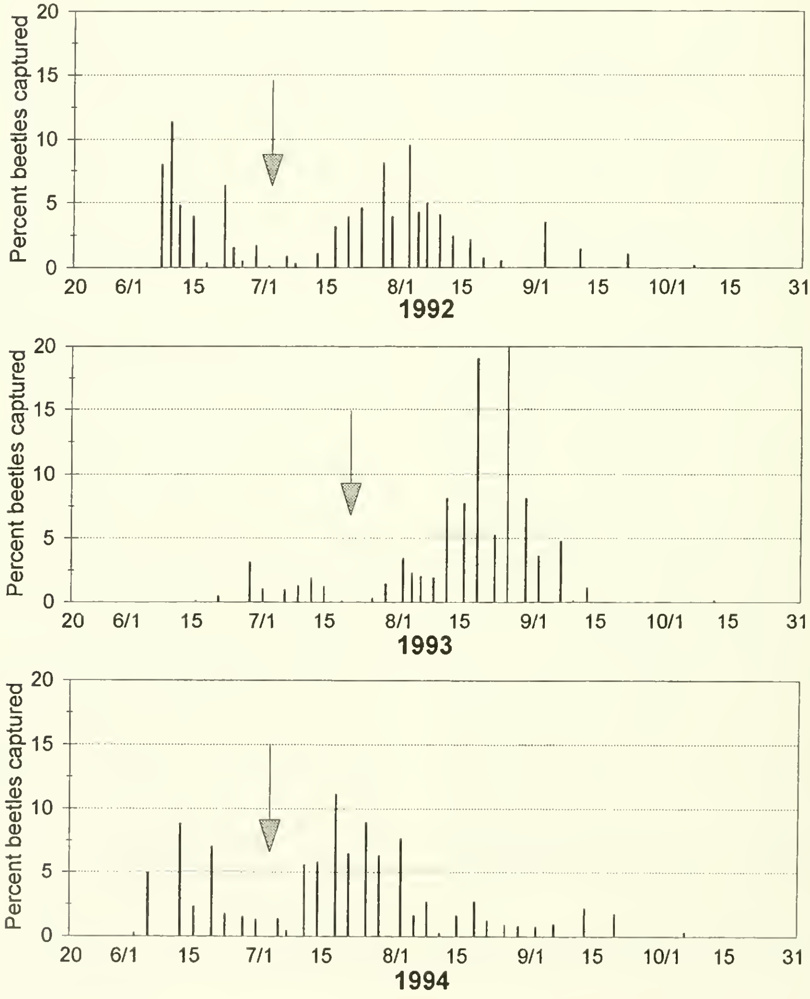

Fig. 2. Percentage of total (n_{1992} = 19,071, n_{1993} = 1800, n_{1994} = 2574) seasonal *Dryocoetes confusus* captures per observation at 2310/2350 m, 20 May–31 October. Arrow indicates the trough between surges not associated with cool or wet weather.

were caught in large numbers throughout June with a 2nd surge of activity in early to mid-August (Fig. 3). *D. confusus* trap captures totaled 9164, with 66% captured in the 1st surge.

In 1993 captures began in late June, peaking in early to mid-July. A 2nd, substantially larger wave started in late July and peaked from mid-August through early September. Captures were about 41% of those in 1992, totaling 3763. Twelve percent of that total were caught in the 1st surge.

The pattern of 1994 captures was similar to that of 1992 with a sharp peak occurring in mid- to late June. A 2nd wave began in late July, peaking in early August. *D. confusus* captures totaled 4476, half of which were caught in the 1st surge.

2600/2660 METERS.—1992 captures began in mid-June with a sharp peak occurring in late June (Fig. 4). A 2nd wave began in late July with a mid-August peak. *D. confusus* captures totaled 7548, with 68% caught in the 1st surge.

In 1993 activity began in late June with an early summer peak in mid-July. A 2nd, substantially larger wave started in late July and peaked from late August through early September. *D. confusus* captures totaled 5882, 16% coming in the 1st surge.

In 1994 activity began in early June with a sharp peak in late June. A 2nd wave began in late July, peaking in early August. Captures were the fewest for any study year, totaling 1331.

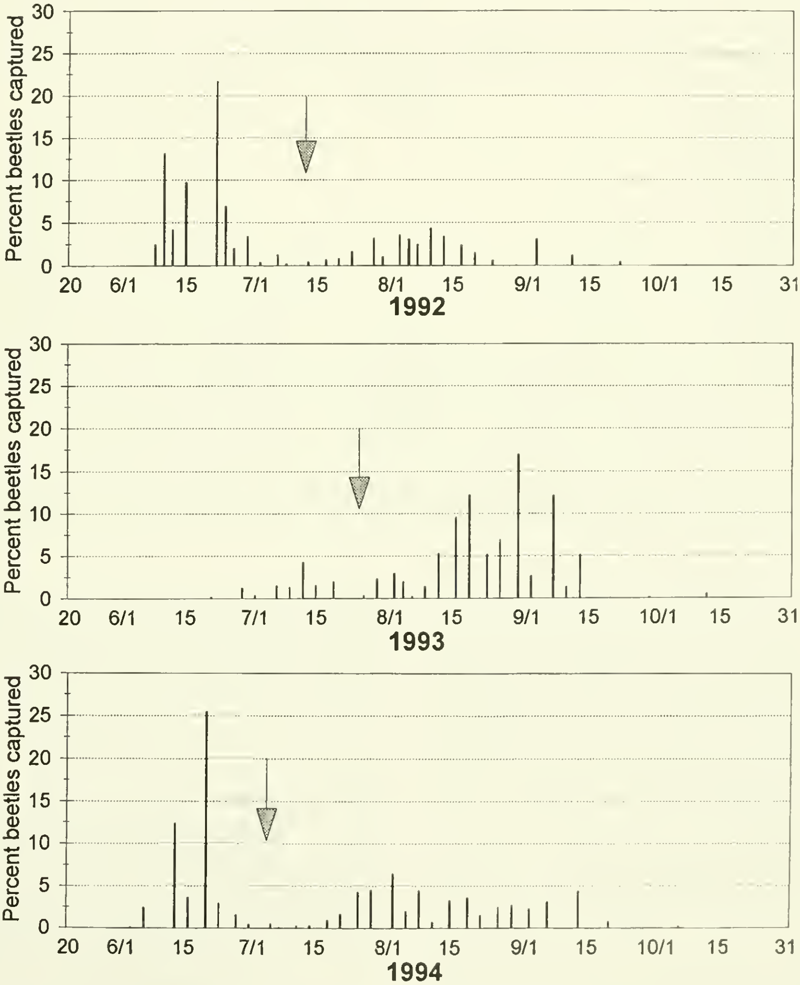

Fig. 3. Percentage of total (n_{1992} = 9164, n_{1993} = 3763, n_{1994} = 4476) seasonal *Dryocoetes confusus* captures per observation at 2560 m, 20 May–31 October. Arrow indicates the trough between surges not associated with cool or wet weather.

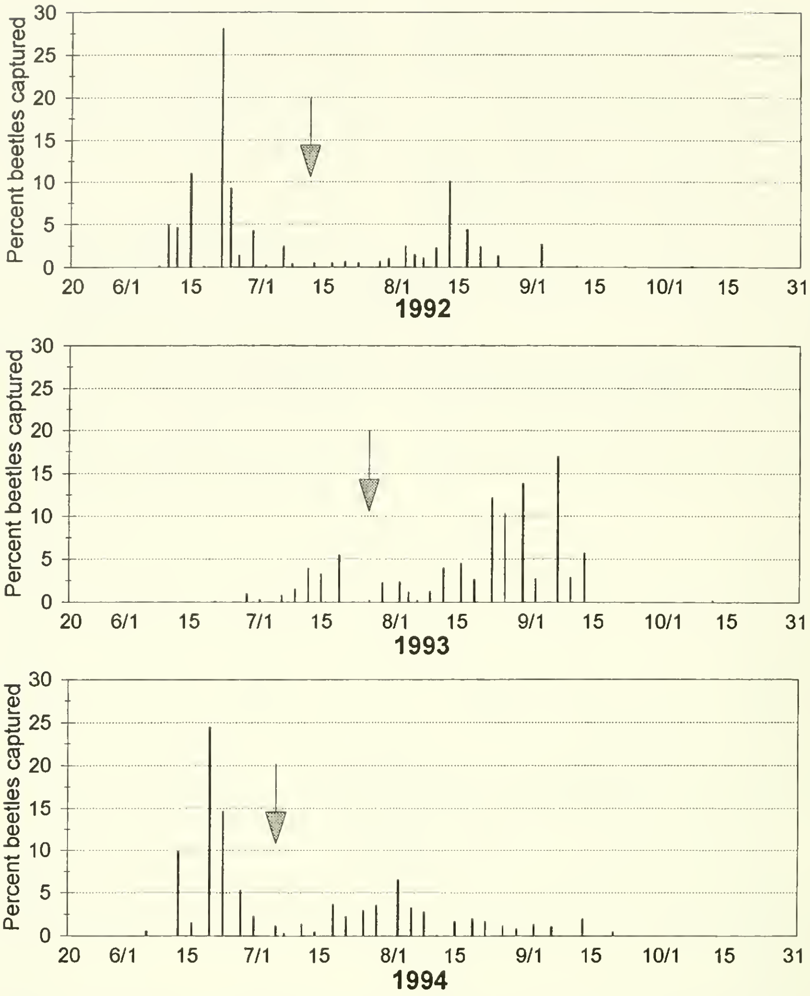

Fig. 4. Percentage of total (n_{1992} = 7548, n_{1993} = 5882, n_{1994} = 1331) seasonal *Dryocoetes confusus* captures per observation at 2600/2660 m, 20 May–31 October. Arrow indicates the trough between surges not associated with cool or wet weather.

Sixty percent of these were caught in the 1st surge.

2840 METERS.—In 1992 the 1st capture was observed on 22 June. Captures peaked in late June, and considerable activity continued through early July (Fig. 5). A 2nd surge occurred in mid- to late August. Captures totaled 17,542 with 72% caught in the 1st surge.

In 1993 activity began in early July with a very large peak occurring in mid- to late July. A 2nd surge occurred in mid- to late August. Captures were down from 1992 levels but were still substantial, totaling 10,344. Seventy-six percent of these were caught in the 1st surge.

In 1994 flight initiated in mid-June with a distinct spike in late June. A late-summer surge began in late July and continued through mid-August. Captures were the greatest of any plot in any year, totaling 20,600. Sixty-seven percent were caught in the 1st surge.

Surge Activity

Considering only the 4 plots common to each study year, there is a trend for the 1st surge to be larger than the 2nd with increasing elevation (Table 1). The lowest elevation plot consistently captured more beetles in the 2nd wave. The highest plot, however, consistently captured more beetles in the 1st surge.

Weather Influences

Periods of cold and/or wet weather coincided with a reduction or pause in beetle

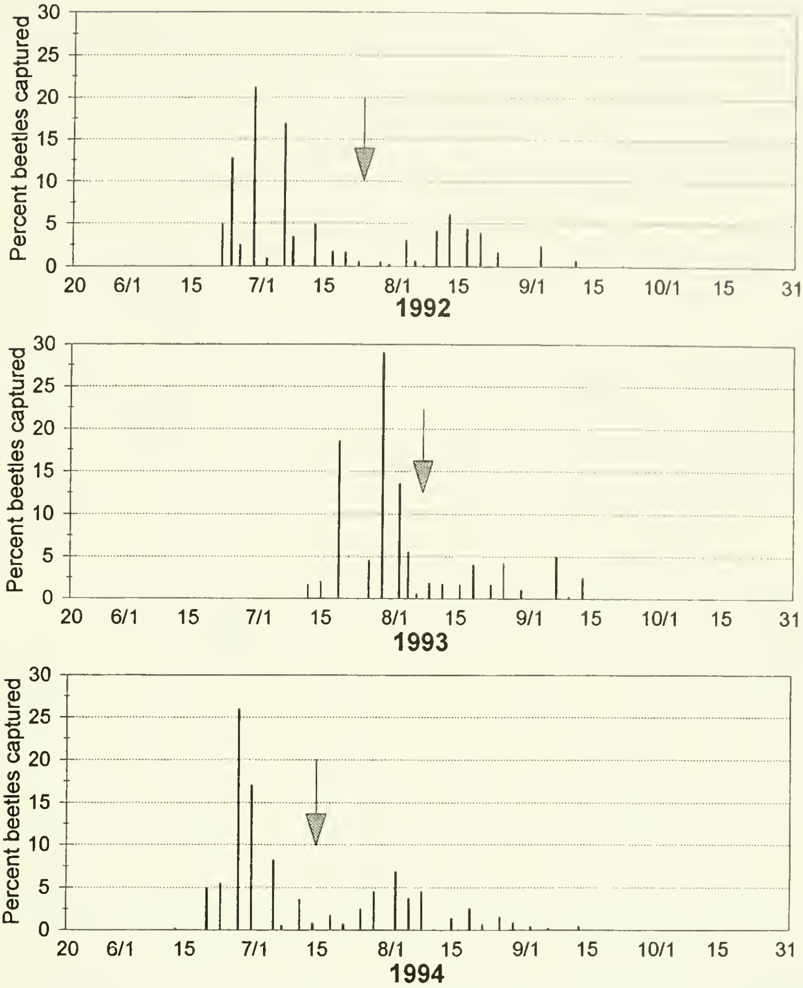

Fig. 5. Percentage of total (n_{1992} = 17,542, n_{1993} = 10,344, n_{1994} = 20,600) seasonal *Dryocoetes confusus* captures per observation at 2840 m, 20 May–31 October. Arrow indicates the trough between surges not associated with cool or wet weather.

captures (Figs. 6–8). Very little flight occurred when daily maximum temperatures were less than 15°C, confirming Stock's (1991) findings. Lapses in flight activity between the main surges, however, are not necessarily associated with cool or wet weather. With 4–7 wk between peaks, warm, dry days were available during these spans of reduced flight.

One would expect delayed emergence and flight timing with increasing elevation. Initial captures at 2840 m were about 2–3 wk later than at 2310/2350 m each year. Timing of peak flight activity was similarly delayed with increasing elevation (Figs. 2–5).

February through May 1992 was the warmest on record for that period in northern Utah. June through August 1993 was the coolest on record while June through August 1994 was the warmest. The warm spring of 1992 coincided with an earlier than expected flight commencement. *D. confusus* were likely flying before trap placement, possibly as early as late May at lower elevations. In contrast, the snowy winter and spring of 1993 followed by a record cool summer resulted in a delayed beetle flight. In 1992 *D. confusus* were first captured at 2840 m on 10 June compared with 6 July in 1993. In each year, regardless of the overall weather regime, I observed that flight did not initiate until the local snowpack was mostly melted and that the early summer peak occurred after all snow patches were gone.

Sex Ratio

The early summer surge typically had a higher portion of male beetles (Table 2). Males were especially dominant during the first 5–10 d of emergence, comprising nearly all of those sampled. The sex ratio then became more evenly mixed for the remainder of the early summer, including during peak activity. The late-summer surge was dominated by females in each year, the ratio being more stable throughout the period.

TABLE 1. Percentage of total seasonal beetle captures per plot occurring in the 1st surge.

Year	Plot (elev. [m])	1st surge (%)
1992	2310/2350	41
	2560	66
	2600/2660	68
	2840	72
1993	2310/2350	10
	2560	12
	2600/2660	16
	2840	76
1994	2310/2350	30
	2560	50
	2600/2660	60
	2840	67

Secondary Scolytids and Predators

Other scolytids captured include *Gnathotrichus sulcatus* LeConte (ambrosia beetle), *Pityokteines minutus* Swaine, *Xylechinus montanus* Blackman, *Hylastes subopacus* Blackman, *Scoly-*

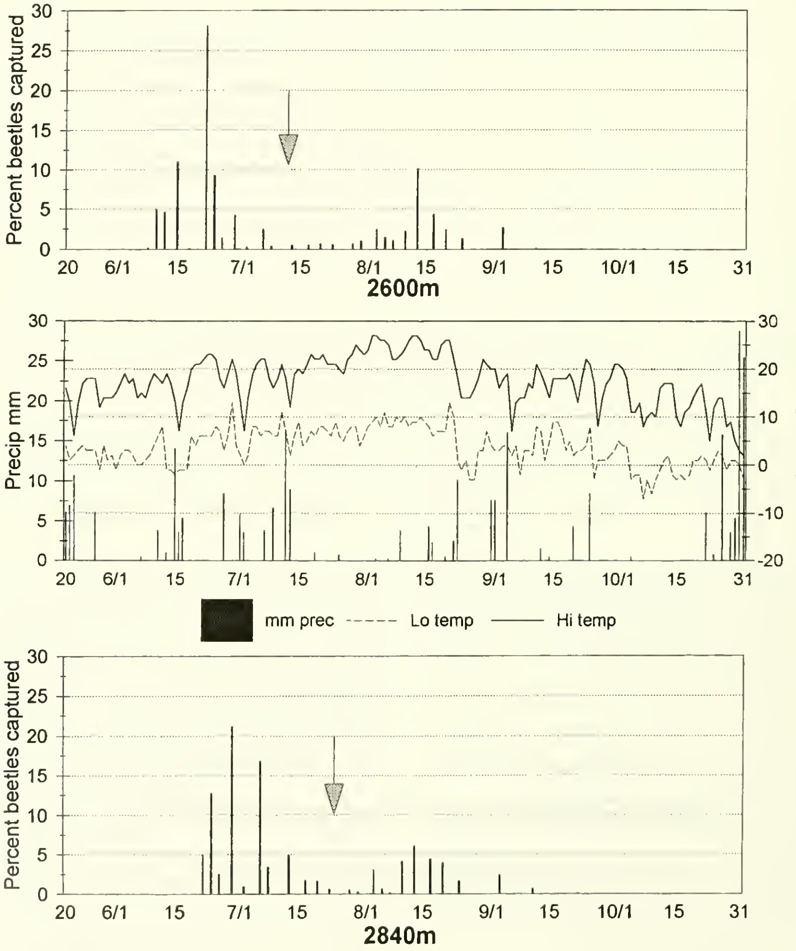

Fig. 6. 1992 daily weather conditions at Brighton–Silver Lake (2700 m) with *Dryocoetes confusus* flight activity at nearby plots. Arrow indicates the trough between surges not associated with cool or wet weather. Note the lag effect, resulting from 2- to 5-d observation intervals, which can give the illusion of flight activity during adverse weather.

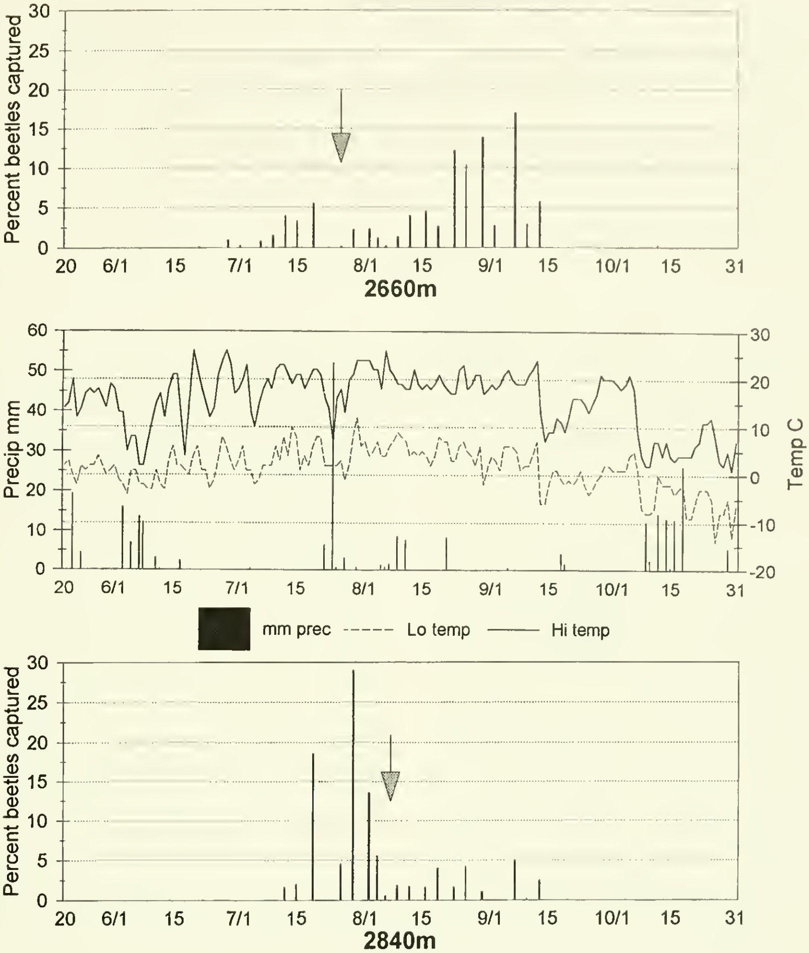

Fig. 7. 1993 daily weather conditions at Brighton–Silver Lake (2700 m) with *Dryocoetes confusus* flight activity at nearby plots. Arrow indicates the trough between surges not associated with cool or wet weather. Note the lag effect, resulting from 2- to 5-d observation intervals, which can give the illusion of flight activity during adverse weather.

tus ventralis LeConte (fir engraver beetle), *Ips* spp., *Cryphalus ruficollis* Hopkins, *Hylurgops porosus* (LeConte), *Scolytus opacus* Blackman, *Dryocoetes affaber* (Mannerheim), and *Dryocoetes sechelti* Swaine. Checkered beetles, *Enoclerus* spp., were the most common and important predaceous insect trapped. Other predators captured include snakeflies (Raphidiidae) and rhizophagids. *Gnathotrichus sulcatus*, *Xylechinus montanus*, *Hylastes subopacus*, *Dryocoetes affaber*, *Enoclerus* spp., and rhizophagids were caught in sufficient numbers to suggest that they possibly cue on *exo*-brevicomin.

Clerids, or checkered beetles (*Enoclerus* spp.), were captured before western balsam bark beetle flight commencement in each year. Captures generally peaked in mid- to late June, then tapered off through August. Few clerids were captured later than the end of August in any year though *D. confusus* continued to be active. At the 4 plot locations common to each study year, a total of 242 clerids were caught in 1992, 357 in 1993, and 307 in 1994.

DISCUSSION

Flight Periodicity

Western balsam bark beetles were caught throughout the summer months for all study years. Beetle flight typically started in June and continued well into September with a few captures as late as early October. Once flight was initiated, only cool or wet weather could

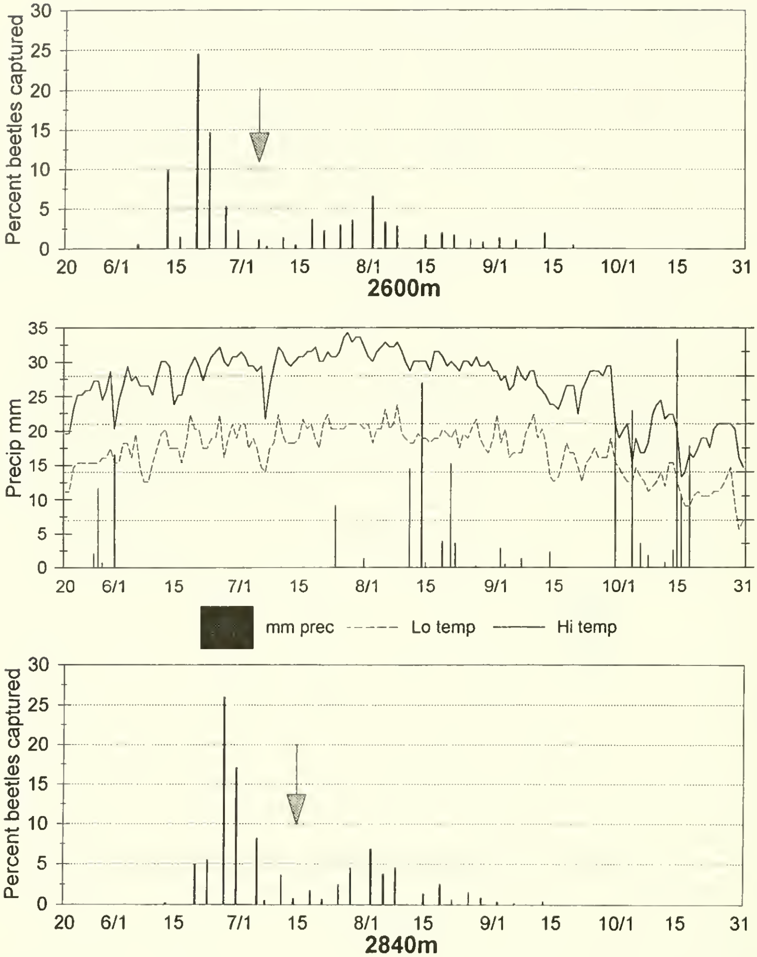

Fig. 8. 1994 daily weather conditions at Brighton–Silver Lake (2700 m) with *Dryocoetes confusus* flight activity at nearby plots. Arrow indicates the trough between surges not associated with cool or wet weather. Note the lag effect, resulting from 2- to 5-d observation intervals, which can give the illusion of flight activity during adverse weather.

completely curtail it. Some warm, dry periods, however, had dramatically reduced activity relative to the peaks. At each plot 2 distinct peaks of flight activity were seen every year. Some plots appeared to have a 3rd peak in September of 1992 and 1994, but this can be attributed to a reduction in trap checking frequency at those times. Generally, the 1st peak was sharp and occurred within 2–3 wk of initial emergence. A 2nd peak was observed 4–7 wk after the 1st.

This is similar to Stock's (1991) findings in British Columbia where there "were two major flight periods per year, the first commencing in mid- to late June, and the second in mid- to late August." Stock found this flight period to correspond well with the life cycle described by Mathers (1931).

Mathers (1931) studied the western balsam bark beetle life cycle at Stanley, B.C., using caged subalpine fir bolts. Young adults were found to emerge and attack fresh trees in June and July. Eggs were laid through August before parents commenced feeding in tunnels before overwintering. Galleries were advanced the following June and July with continued egg laying. Parents then reemerged in July to attack a fresh host with a 3rd set of brood tunnels excavated, eggs being laid through August. Mathers concluded this to be the end of the life cycle. Eggs from the 1st brood overwintered as larvae before pupating the following summer. The 2nd winter was passed as young adults that emerged to attack fresh trees the following June and July. Eggs from the 2nd and 3rd broods overwintered as larvae that pupated the

TABLE 2. Percentage of females among sampled beetles in early and late-summer surges.

	1993		1994	
Plot (elev. [m])	1st surge (%)	2nd surge (%)	1st surge (%)	2nd surge (%)
2310/2350	47	74	38	51
2560	46	71	29	60
2600/2660	34	75	28	66
2840	52	64	44	60

following year and emerged as adults the next season. Given this life cycle, one would expect to find all life stages represented in any given year. Stock (1991) suggests that the August peak observed in his study corresponds to the July reemergence described by Mathers, the timing difference due to warmer conditions at Mathers' site. Using Mathers' life cycle, the 2 flight peaks must be of different generations, the June peak being of newly emerged young adults and the August peak being of reemerged 2nd-yr adults. This gives a 3-yr life cycle when the reemergence year is included. Beetles from eggs laid in 1991, for example, presumably might not complete their life cycle until 1994.

Bright (1963) suggests that parent beetles may die in their 1st or 2nd brood tunnels before reemerging to attack another host. This would account for the late-summer surge often having less activity than the early summer surge. Bright also believes *D. confusus* to have a 1-yr life cycle in the western United States, the life cycle proposed by Mathers (1931) being a phenomenon restricted to the insect's northern range. No data or references, however, are cited for this assertion.

The flight period data presented here produced noticeably different results each year. This is almost certainly associated with the record-setting weather regimes seen each study year. The double peak pattern was not as evident during the cool, wet summer of 1993. Only the highest elevation plot exhibited a large, early summer peak, July in this case. The lower elevation plots had a noticeably reduced early summer peak. The greatest activity at these plots occurred in late August. The record cool summer weather likely caused the delayed emergence seen in 1993, but this does not explain the diminishment of the early summer peak. Even with delayed development, I expected considerable activity once flight was initiated. Cold weather during emergence was explored as a possible cause for the reduction in the early summer peak. Night temperatures at 2700 m dropped to –4°C on 24 June 1993, which could have killed some new adults and further delayed the early summer flight (Barbara Bentz[6] personal communication). Perhaps development of some new adults was delayed such that their emergence overlapped with that of reemerged adults in the late summer.

At the highest plot, Mathers' (1931) hypothesized life cycle corresponds well with the data. The 2nd and 3rd broods described by Mathers would assure an early summer surge each year even though 2 yr is required for sexual maturity. In other words, there is no "off year" such as with the 2-yr life cycle of the spruce beetle, *Dendroctonus rufipennis* (Kirby).

Some results from this study did not match Mathers' (1931) life cycle as well as did Stock's (1991). For example, assuming that the same local population was sampled each year, adults in the early summer flight of 1993 should be represented again in the late-summer flight of 1994. Allowing for some degree of mortality, I expected the late-summer surge to have fewer beetles than the early summer surge of the previous year for a given location. This study produced 2 examples where the late-summer surge contained several times *more* beetles than the early summer surge of the previous year. If, in fact, these plots did sample the same populations each year, then Mathers' (1931) life cycle may not be accurate for northern Utah.

Though funnel trap captures are not appropriate for adequately describing a life cycle, there are several possible explanations for the unexpected results at the 3 lower plots. The record-setting weather regimes in each year would have certainly affected beetle phenology. Perhaps some critical thresholds were not achieved in 1993, resulting in retarded development or mortality (Barbara Bentz personal communication). This may have affected young adults more so than reemerging adults. Conversely, record warm weather in 1992 and 1994 could have advanced development. Perhaps the 2nd and 3rd broods are not important in the overall life cycle. Amman and Bartos (1991) found reemerged mountain pine beetle, *Dendroctonus ponderosae* Hopkins, females to produce significantly fewer offspring than new females with males. Perhaps lower elevation beetles tend to have a 1-yr life cycle while 2 yr is required for beetles at higher elevations. Probably some combination of these factors plus some not explored, such as disease and predation, contributed to the results.

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Sex Ratio

Stock (1991) found that the late-summer surge is comprised largely of females. Using August 1 to distinguish 1st and 2nd flight, Stock found females to comprise 48%, 29%, and 50% of the 1st flight during 3 consecutive years. The 2nd flight had 80%, 48%, and 66% females. I found similar trends in northern Utah. This predominance by females during 2nd flight is typical for other scolytids that exhibit reemergence (Anderbrandt et al. 1985, Flamm et al. 1987). This suggests that the late-summer surge, in fact, comprises reemerged adults. The dominance of males during the initial days of early summer emergence suggests that they are likely responsible for host selection and mate attraction.

Weather Influences

Stock (1991) found the majority of western balsam bark beetle flight to occur when the daily maximum temperature was greater than 15°C. The same trend is seen here. Periods of cool weather, especially when coupled with precipitation, essentially stopped beetle captures. Given warm, dry days, *D. confusus* was found to be active as late as early October, albeit in greatly reduced numbers. Any control strategy will need to consider this extended flight period.

Surprisingly, the cool, wet summer of 1993 failed to have any obvious effect on the 1994 beetle population other than to delay emergence. I hypothesized that this weather pattern would have increased beetle mortality, resulting in fewer trap captures in 1994. Elsewhere in the region, mountain pine beetle larvae were observed with retarded development, possibly leaving overwintering life stages more vulnerable to cold weather mortality. Assuming a 2-yr life cycle for western balsam bark beetle, perhaps the more cold-susceptible life stages would not have emerged until June 1995. It is also possible that winter temperatures in 1993–94 did not reach lethal levels.

While early emergence was associated with a record warm spring in 1992, the early summer peak was no earlier than after the more typical spring of 1994. Timing of the early summer peak for each plot occurred on essentially the same date in 1992 and 1994. Timing of the late-summer peak, however, was about 2 wk earlier during the record warm summer of 1994 than the more typical summer of 1992.

CONCLUSION

Once flight begins, activity typically builds to a sharp peak within 2 wk. This generally occurs from mid-June through early July. Activity then subsides before building to a 2nd peak 4–7 wk later, usually in August. Significant activity can continue into early September with some beetles flying as late as early October.

Cultural or semiochemical management of western balsam bark beetle will need to consider the double peak flight pattern of parent beetles and the fact that adult beetles can be found in some quantity throughout the warmer months. Removal of infested host material, for example, should be done in the fall when flight is complete. Anti-aggregation pheromones will need to be formulated to effuse up to 4 mon or, possibly, applied twice per season.

Further research is needed to confirm or revise the life cycles described by Mathers (1931) and suggested by Bright (1963) since control strategies for a 1-yr life cycle can be different from a 2- or 3-yr life cycle. Considering the 1st versus 2nd surge differences, this should be done for a range of elevations. The role of reemerged adults in brood production must be determined for a more complete understanding of the overall life cycle. The conditions leading to an outbreak also need to be quantified such that cultural guidelines can be established.

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DISTRIBUTION OF A THERMAL ENDEMIC MINNOW, THE DESERT DACE (*EREMICHTHYS ACROS*), AND OBSERVATIONS OF IMPACTS OF WATER DIVERSION ON ITS POPULATION

Gary L. Vinyard[1]

ABSTRACT.—Population status surveys were performed from 1987 to 1996 for desert dace (*Eremichthys acros*), a cyprinid endemic to several small thermal springs in Soldier Meadow, Humboldt County, Nevada, where the species occupies 7 spring areas in a single valley. Because spring distributions are patchy and all areas are not linked by surface flow, each area comprises a more-or-less isolated population, although irrigation practices or high runoff may occasionally link several of them. Although limited to thermal springpools and outflows, desert dace were found in temperatures ranging from 37°C near spring sources to 13°C in downstream areas. Between May 1988 and October 1989, most of the discharge from a major spring outflow was diverted from its natural channel into an irrigation ditch. Trap catches in the original channel were reduced after the diversion, and fish densities were lower in the ditch than in the channel. Reduced fish numbers still persist (1996), even though the affected site has been relatively undisturbed since 1989. To improve desert dace habitat and increase populations, irrigation diversion should be discontinued and water returned to the original channel. Continued protection and increased habitat preservation for desert dace are recommended because of their limited distribution, apparently restricted habitat requirements, and the potential for environmental disruption in the area.

Key words: conservation, endemism, Eremichthys acros, *Great Basin, habitat, irrigation, Nevada, springs.*

The desert dace (*Eremichthys acros*, Cyprinidae) is a federally listed threatened species restricted to outflows of thermal springs in Soldier Meadow, Nevada (Hubbs and Miller 1948, La Rivers 1962). Desert dace have a unique horny sheath on both jaws and a greatly elongated intestine; they occupy exceptionally high temperatures relative to other cyprinids (Hubbs and Miller 1948, Nyquist 1963). The distinctive morphology of desert dace suggests a long period of isolation extending beyond the most recent pluvial period. The desert dace differs significantly from other Great Basin minnows, and its original description and assignment to a monotypic genus (Hubbs and Miller 1948) have been confirmed (La Rivers 1962, Nyquist 1963, Cavender and Coburn 1992). Its taxonomic relationship within the western cyprinid fauna remains unclear, and recent workers have judged desert dace most similar to either relict dace, *Relictus solitarius* (Cavender and Coburn 1992), or to tui chub, *Gila* (*Siphateles*) *bicolor* (Lugaski 1980).

Few investigations of desert dace have been undertaken since Nyquist (1963), and little is known of their behavior, ecology, or physiology. I present results of studies of desert dace distribution and document adverse consequences to the species from water diversion in the valley.

STUDY AREA

Soldier Meadow and Mud Meadow to the south occupy a gently sloping valley in southwestern Humboldt County, Nevada. Elevation ranges from about 1400 m MSL at the north end of Soldier Meadow to about 1317 m MSL south of Mud Meadow Reservoir (Fig. 1). Although the lower elevations are near maximum shoreline level of pluvial Lake Lahontan, the area was probably not inundated during the Pleistocene (Benson 1978). Soldier Meadow is also home to an endemic plant, the basalt cinquefoil (*Potentilla basaltica*), and at least 4 undescribed species of hydrobiid springsnails (R. Hershler, Smithsonian Institution, personal communication).

Ranching operations in Soldier Meadow began in the late 1860s but have never been particularly successful. After an active period in the 1960s, ranching was largely dormant in the valley through most of the 1970s and early 1980s. In 1994, with the help of the Nature Conservancy, much of the property was transferred to

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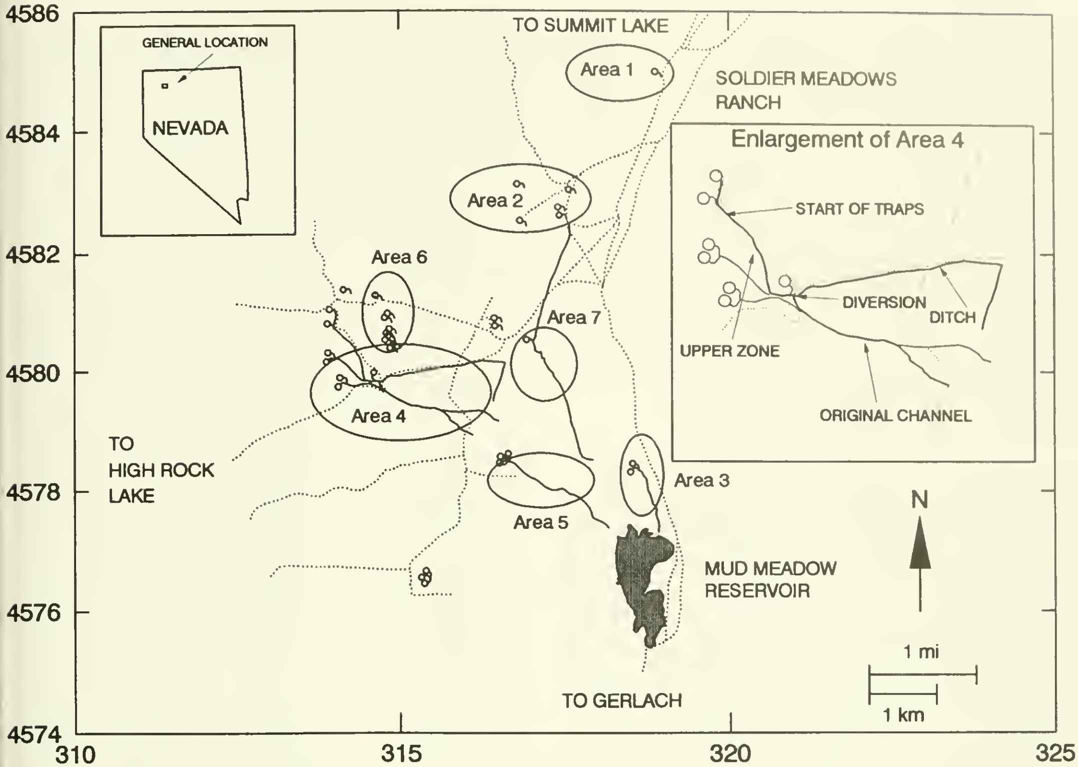
4586
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GENERAL LOCATION
NEVADA
TO SUMMIT LAKE
Area 1
SOLDIER MEADOWS RANCH
Enlargement of Area 4
START OF TRAPS
DIVERSION
DITCH
UPPER ZONE
ORIGINAL CHANNEL
Area 2
Area 6
Area 7
Area 4
TO HIGH ROCK LAKE
Area 3
Area 5
N
MUD MEADOW RESERVOIR
1 mi
1 km
TO GERLACH

Fig. 1. Map of Soldier Meadow and Mud Meadow showing sampling locations. Solid lines indicate water courses; dotted lines are roads. Spring areas discussed in the text are enclosed in ovals. Not all springs in the valley are presented, and in some areas numerous small springs are represented by single symbols. Springs and streams outside the ovals lack desert dace (*Eremichthys acros*), but not all sites within ovals contain fish. Values on axes indicate coordinates in relation to 1000 meter Universal Transverse Mercator Grid, digitized from USGS maps. Insets show location of Soldier Meadow in relation to Nevada state boundary (left) and an enlargement of the spring and ditch system associated with area 4 (right). The area 4 inset depicts the relationships between the spring sources, upstream zone, ditched zone, and old channel as discussed in the text. The ditch was most recently dredged between May 1988 and October 1989. The approximate upstream limit of desert dace was near the start of the traps.

the U.S. Bureau of Land Management. Most desert dace habitat now occurs on public land, and the remainder of the privately held habitat is protected by a conservation easement (Nature Conservancy 1994). Springs and outflow streams in the valley are all subject to grazing by cattle, feral horses and burros, and pronghorn. There is also frequent recreational use of the area by hunters, campers, bathers, and others.

Fish Distribution

Desert dace distribution is strongly correlated with spring discharge. Fish are absent from small springs or seeps with little surface water and from larger pools of very hot water lacking organized discharge. All springs with perennial surface flow are occupied by desert dace, the most abundant fish in the valley. Although desert dace are most often found in habitats lacking other fish species, they are not confined to them and have been observed coexisting with tui chub, speckled dace (*R. osculus*), and Tahoe suckers (*Catostomus tahoensis*; La Rivers 1962, Nyquist 1963, Sigler and Sigler 1987).

Desert dace habitat occurs in 7 distinct areas located within an 8-km (5-mi) radius (Fig. 1). Because spring distributions are patchy and all areas are not linked by surface flow, each area comprises a more-or-less isolated population, although irrigation practices or exceptionally high runoff may occasionally allow fish passage among several of them. Most areas described below contain many springs varying greatly in size, and it is often difficult to identify the exact number and location of discharge sources because of the dense vegetative cover.

Area 1

Area 1 (Fig. 1) includes the type locality (Hubbs and Miller 1948) for desert dace (Table 1, site 19), a spring that issues from the base of a small cliff. It is modified by a valved structure diverting flow into a pipe for household use at Soldier Meadow Ranch. Undiverted discharge flows about 100 m east, where it enters a small impoundment or a series of irrigation ditches. Desert dace coexist with tui chub in the spring and impoundment. Desert dace habitat here is limited by the impoundment and by the shifting diversion into ditches.

Area 2

In area 2 (Fig. 1) several small springs containing desert dace (Table 1, sites 9, 23–27) are located around the base of a small hill and flow generally southward or southwestward into a large meadow. A large springpool containing desert dace (Table 1, site 10) is the largest naturally occurring body of open water in the valley (approximately 15 m in diameter and 1.5 m deep). It has a minor surface outflow south into a marshy meadow. Normally, most of the springs in this area are unconnected, although proximity and common drainage suggest connections are likely during high runoff. Natural drainage from this site is toward area 7, and the outflows of several of the more southerly springs are ditched southward through the meadow. The larger springs in this area receive frequent recreational use by bathers and campers.

Area 3

Area 3 (Fig. 1) includes several small springs flowing south approximately 1 km north of Mud Meadow Reservoir (Table 1, site 20). Although at least 3 springs in this area contain desert dace, and some populations are quite dense, all springs in the area have been heavily affected by livestock grazing and irrigation diversion. The 2 largest springs have long been diverted into irrigation ditches at a point within 20 m of the sources. Grazing by cattle, burros, and feral horses has altered the vegetation and disrupted soils near the springs. This disturbance has widened the outflow channel, reduced water depth, and generally eliminated riparian vegetation.

Area 4

Several large springs issuing from the side of a small hill are the source for area 4 (Fig. 1). With more than 2600 m of stream, this is the largest contiguous potential habitat for desert dace. Water issues from the highest springs at approximately 50°C (Table 1, sites 1–6, 11, 21) and cools gradually while flowing downstream with occasional augmentation by both warm and cool inflows. These springs produce an aggregate discharge of approximately 60 l/s. The upper reaches are fishless, presumably because of high water temperatures. Headwater springs in area 4 probably receive the highest level of recreational use in the valley, primarily from bathers and campers. Several small cobble dams erected across the outflow stream in this area are mostly upstream from the dace habitat and pose little impediment to fish passage. Deposition of soaps and other water pollutants from bathers may constitute a risk of unknown magnitude. This area has also been heavily grazed by cattle and feral horses and burros.

Several irrigation diversions have long existed in area 4; however, they were poorly maintained and little used for at least a decade. Between May 1988 and October 1989, the rancher in the valley dredged out an old ditch, moving water away from the original channel in area 4 (Fig. 1, inset). Before the dredging most of the discharge continued southeastward in the natural channel and spread into a large, wet meadow. Speckled dace historically coexisted with desert dace in the lower sections of this system near the wet meadow.

By October 1989 most discharge in area 4 was diverted east to the irrigation ditch, and no water reached the meadow by the original channel. Currently, approximately 80% of the total combined discharge from the source springs in area 4 is diverted. Speckled dace are now absent from the system, and the amount of desert dace habitat was significantly reduced by this diversion. The loss of discharge into the lower portions of the wet meadow on the downstream end of area 4 had additional adverse impacts on desert dace in area 5 (see below).

Area 5

Area 5 includes a group of very hot springs that enter a series of old irrigation ditches approximately 200 m from the source and then flow southeasterly toward Mud Meadow Reservoir (Fig. 1). In 1988 a series of cool springs fed by discharge from the wet meadow below area 4 entered the outflow stream at area 5 approximately 50 m downstream from the primary spring sources. Mixing of these waters produced

TABLE 1. Characteristics of spring habitats in Soldier Meadow. Data were collected at various times between 1987 and 1995. Column designations are as follows: AREA = distribution area (numbers indicate areas indicated on Figure 1, sites without numbers lack desert dace); SITE = site identifier from field notes, refers to specific locations within areas, EAST and NORTH indicate site locations in relation to 1000 meter Universal Transverse Mercator Grid, digitized from USGS maps—Mud Meadow, 1972; Soldier Meadow, 1972; FISH = fish species present, E = *Eremichthys acros*, R = *Rhinichthys osculus*, G = *Gila bicolor*, C = *Catostomus tahoensis*, a = fish absent; °C = water temperature; DO = dissolved oxygen concentration (mg O_2/l); COND = electrical conductivity (μMho/cm).

AREA	SITE	EAST	NORTH	FISH	°C	DO	COND
1	19	318885	4584932	E,G	28-29	5.6-6.2	190
1	19A	319038	4584990	E,G	22-26	8.0-8.6	190
2	9	317625	4583030	E	34-38	3.4-4.5	432
2	10	316826	4582540	E	21-34	4.8	410
2	23	317547	4582650	E	21		
3	20	318607	4578372	E,R	25	4.5-6.1	270
4	21	315827	4580116	E	17		
4	1	314016	4580934	a	36-40	3.6-5.8	370-420
4	2	314068	4580654	a	36-38	5.3-5.8	380-420
4	3	314446	4579892	E	30-35	6.2-6.4	310
4	4	314869	4579580	E	27-28	6.4-7.0	
4	5	314005	4580202	a	37-42	1.8-3.7	400-430
4	6	315961	4578982	E,R	19-25	5.8-7.6	280-285
4	11	315331	4579392	E	20-29	6.3-8.0	305
5	12	316691	4578454	E	13-50	1.9-6.3	480
5	13	316888	4578154	E,R	23	6.1	650
5	14	317089	4577836	E,R	23	5.6	650
6	16	314599	4581304	E	23	6.5	295
7	8	316929	4580550	E	34-57	0.9-6.9	470-750
—	7	316682	4580660	R,C	6	8.3	325
—	15	315512	4576460	a	25	5.6	280
—	17	314198	4581512	a	35	3.6	370
—	18	316939	4580684	a	50	3.8	280
—	22	317115	4581286	R	13		
—	24	317536	4582660	a	35		
—	25	317519	4582660	a	37		
—	26	317498	4582640	a	40		
—	27	317516	4582620	a	40		
—	28	316383	4580864	a	10	8.9	
—	29	316381	4580940	a	9	5.5	

steep temperature gradients, as waters of ±45°C and <20°C gradually mixed over about 100 m. In May 1988 water in the main spring outflow was 43°C at the point where water at 13°C entered from the meadow to the north. Desert dace were observed actively feeding in the 13°C water mass at the point where cold water entered the primary channel. Fish also darted into the turbulent zone between the hot and cold water masses in pursuit of small drifting food. All observations since October 1989, after the diversion of water in area 4, have found the amount of water reaching the lower sections of the wet meadow above area 5 to be greatly reduced, and inflow from the cool springs flowing into area 5 has ceased. Consequently, several hundred meters of the approximately 1100 m of (ditched) desert dace habitat have been lost from this area. This area is grazed and the outflow ditched, but it receives relatively little recreational or other use.

Area 6

The desert dace population in area 6 (Table 1, site 16, Fig. 1) occupies a single spring stocked by U.S. Bureau of Land Management personnel in the early 1980s at a time of concern over the future of desert dace. This spring has the smallest discharge of any containing desert dace (estimated at less than 5 liters per minute). A gauging box and wooden notch weir produce a small impoundment (approximately 3 m × 3 m) about 30 m from the source, which contains most of the fish population at this site. Recently this impoundment was nearly lost by deterioration of the weir. This system also includes a somewhat larger earthen impoundment (±10 m diameter) approximately 50 m from the source, after which flow disappears into a small meadow. Desert dace are mostly restricted to the area above the larger impoundment and are most abundant near the gauging box and notch weir. This site is grazed but too small for recreational use.

Area 7

Area 7 includes several hundred meters of suitable habitat fed by several springs on the eastern side of the valley (Fig. 1). Because several springs issue at temperatures exceeding 50°C, the extent of suitable habitat varies with ambient air temperature. This area may be connected with outflows from area 2 during periods of high runoff. Most of the outflow in this area has been modified to some extent for irrigation, and it is subject to grazing and some recreational use.

Mud Meadow Reservoir

Mud Meadow Reservoir contains largemouth bass (*Micropterus salmoides*), goldfish (*Carrasius auratus*), and perhaps other species planted by unknown individuals (Ono et al. 1983). It is unclear whether it is a barrier to desert dace passage, but it is unlikely to provide any permanently suitable habitat. Although no nonnative fishes have been observed in any sites containing desert dace, the potential threat posed by nonnative fishes spreading into dace habitat is certainly enhanced by their establishment in the reservoir.

MATERIALS AND METHODS

All desert dace habitats recorded by Nyquist (1963) and most other springs in the valley were visited in 1987 to update distribution information (Vinyard 1988). The dredging of the irrigation diversion in area 4 significantly reduced the amount and quality of desert dace habitat in that area. Investigations thus were concentrated in the affected locality (area 4) beginning in 1989.

Fishes in area 4 were sampled with standard unbaited minnow traps on 5 occasions (14 May 1988, 20–22 October 1989, 3 November 1993, 20–21 October 1995, and 27 April 1996). During May 1988 sampling included the entire original stream channel (>2.6 km) from spring sources to disappearance of the stream in a wet meadow. The section upstream from the diversion and the irrigation ditch were sampled in October 1989, November 1993, October 1995, and April 1996. The remnant natural channel downstream from the diversion was also sampled in October 1995 and April 1996 (Fig. 1, inset).

Fish traps were 40 cm long by 20 cm diameter, constructed of 0.64-cm-mesh galvanized hardware cloth, with 2.5-cm entrance holes at the peak of each concave conical end section. Traps were placed at 20-m intervals along spring outflows and fished 2 h during daylight. Although the traps were sometimes not completely submerged, they were always placed with the openings under water. Captured fishes were identified, enumerated, and released near the point of capture. Standard length (SL, in mm) and weight (gm) were recorded on some sample dates. Water temperature, dissolved oxygen, and electrical conductivity were measured using portable meters at regular intervals along the trap set.

In October 1995 stream velocity was measured along cross-section transects with a Marsh-McBurney model 201D flow meter at 6 or 9 sites each in the upstream, ditch, and old channel zones of area 4. Measurements were at 5-cm vertical and either 10- or 20-cm horizontal increments, depending on channel width.

In June 1995 electrofishing was performed using a 3-pass depletion methodology (Van-Deventer and Platts 1989). Stream sections 10 m long were isolated with blocking nets and depletion rates on successive passes used to estimate population size. Three groups of 6 sections were fished: in area 3, and in the old channel and ditched zones of area 4.

RESULTS

Although resident in thermal springs and outflows, desert dace have wide temperature tolerances and were observed in waters ranging from 13°C to 38°C. Occupied waters had conductivity ranging from 190 to 650 μS and dissolved oxygen concentrations generally near saturation, ranging from 4.5 mg/l to 8.0 mg/l (Table 1). Although there was considerable overlap between species, desert dace were found at higher temperatures and lower dissolved oxygen concentrations than speckled dace, which were not observed at temperatures above 26°C or in dissolved oxygen concentrations below 5.2 mg/l.

In area 4 in 1988 desert dace catch in minnow traps was significantly negatively correlated with temperature (linear regression; $F = 19.98$, $R^2 = 0.122$, $n = 131$, $P < 0.001$), although relatively little variance in catch was explained by temperature, and no such correlation was observed in later years. Desert dace catch was also not significantly correlated with speckled dace catch. Catch rates generally reflect fish abundance but may also be affected by activity. Temperature, dissolved oxygen concentration, and combinations of these and other factors may affect activity levels.

In 1988, when desert dace and speckled dace were sympatric in the natural channel above the meadow in area 4, mean catch per trap-hour was significantly greater ($t = 2.83$, $P = 0.009$) for desert dace (4.56 fish per trap-hour) than for speckled dace (1.04 fish per trap-hour). Where both species occurred, desert dace was more abundant, and maximum densities of both species were observed at temperatures of about 23°C.

Cross-section grid transect measurements of water velocity were used to assess mean values at each transect and to compute discharge. In 1995 in area 4, velocities were significantly higher in the ditch (6 transects, $\bar{z} = 24.9$ cm/s, $n = 121$) than in the upstream zone (9 transects, $\bar{z} = 17.3$ cm/s, $n = 318$; t test, df = 159, $T = -3.663$, $P < 0.001$), or in the old channel (6 transects, $\bar{z} = 16.7$ cm/s, $n = 111$; t test, df = 188, $T = 3.733$, $P < 0.001$). However, velocity measurements did not differ significantly between the upstream and old channel segments (t test, df = 226, $T = 0.504$, $P = 0.616$). Volumetric computations indicated that discharge in the ditch was 46.5 l/s while discharge in the channel was 10.8 l/s, or 18.8% of the total.

In October 1995 desert dace trapped in the upstream zone were significantly smaller (mean SL = 35.9 mm, $n = 172$) than those from either the ditch (mean SL = 38.7 mm, $n = 82$; t test, df = 105, $T = -3.33$, $P = 0.001$) or the old channel (mean SL = 38.4 mm, $n = 135$; t test, df = 284, $T = -5.50$, $P < 0.001$). Standard length of the fish in the ditch and in the old channel did not differ significantly (t test, df = 113, $T = 0.328$, $P = 0.744$).

Electrofishing transects in area 4 June 1995 yielded mean values of 21.8 fish per 10 m ($n = 6$, $s = 27.2$) for the old channel and 12.5 fish per 10 m ($n = 6$, $s = 8.5$) for the ditch zones. Density estimates of 110 fish per 10-m section ($n = 6$, $s = 51.53$) were obtained in area 3 at that time. These values did not differ significantly among the 2 zones of area 4; however, densities in area 3 were significantly higher than in either zone of area 4 (t tests, $P < 0.01$ in both cases). The fish electrofished from the ditch were significantly larger (avg. SL = 37.2 mm, $n = 67$, $s = 7.9$) than those from the old channel (avg. SL = 32.7 mm, $n = 122$, $s = 11.3$; t test, $t = 3.2$, $P = 0.002$).

DISCUSSION

Trap data from area 4 offer an opportunity to assess impacts of habitat alteration by comparing catch rates in the zone upstream from the diversion, in the original channel downstream, and in the ditched zone (Fig. 2). Because traps were set on the same spacing intervals in each sampling period, it is possible to examine cumulative catch per trap hour to compare fish densities. These values are computed by summing catch per trap hour for each trap along the trap set from the upper to the lower end (Fig. 2).

The total cumulative catch in area 4 was much larger in May 1988 than at any other time (Fig. 2). In contrast, the lowest cumulative catch observed was in October 1989, the first sample after the ditch dredging. Although direct comparisons of these 2 samples may be confounded by seasonal differences, the contrast between the largest catch observed (in May 1988) and the smallest catch observed (in October 1989) coincides with the dredging. Comparison of the autumn sample in October 1995 with the spring sample in April 1996 suggests that populations are larger in the spring than fall, but that this difference is probably insufficient to explain the difference between the 1988 and 1989 data.

By November 1993 the cumulative catch had recovered somewhat from 1989 (Fig. 2). A notable difference in 1993 relative to both earlier observations was the sharp increase in catch apparent at about 1000 m, slightly upstream from the diversion. However, with the exception of the accumulation of fish at this point, the general slope of the cumulative catch curve was little changed from October 1989. In October 1995 and April 1996 sharp increases in catch immediately above the diversion were still apparent. The general slope of the catch

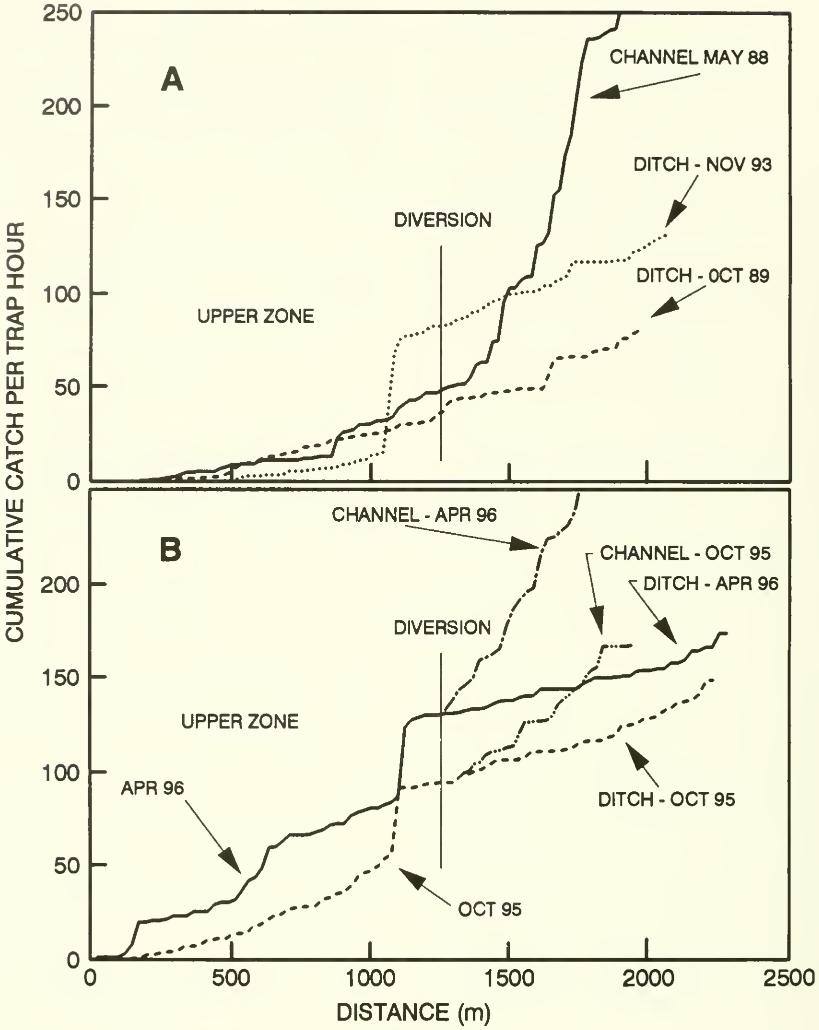

Fig. 2. Cumulative catch of desert dace in unbaited minnow traps in area 4 from May 1988 through April 1996: A, Data collected in May 1988, November 1993, and October 1989. B, Results from 1995 and 1996. In all cases single, unbaited minnow traps were fished at 20-m intervals for 2-h sets during daylight. Cumulative catch per hour is computed by summing catch per hour for each trap beginning at the upstream end of the trap set. Distance on the ordinate is the distance downstream from the first trap. In May 1988 cumulative catch reached 448 at 2620 m downstream (off scale). Dredging of the irrigation diversion occurred between May 1988 and October 1989. Samples in October 1988 and 1993 included only the zone upstream above the diversion and the ditched zone downstream. In October 1995 and April 1996, the old channel remaining below the diversion was also sampled.

curve for the ditched segment changed little between 1993 and 1996 (Fig. 2). The slope from the remnant old channel in 1995 and 1996 (Fig. 2) was much steeper than that observed in the ditch, in spite of the roughly 4 times greater discharge measured in the ditch in 1995. Catch rates in the ditch or old channel have never reached levels observed in the channel in 1988, and even summing the cumulative catch from both the ditch and the old channel still does not yield results comparable with the catch rates observed in 1988.

Different responses by desert dace to the various habitats in area 4 are also evident in the percentage of traps with non-zero catch (Fig. 3). This measure can be used as an indirect indication of the amount of habitat occupied. In 1988 the channel zone had the highest percentage of traps catching fish, nearly 90%. In the 4 samples from the ditched segment,

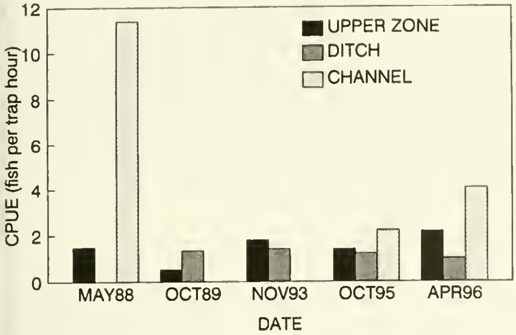

Fig. 3. Average catch per trap hour for all traps, area 4, from May 1988 through April 1996. Bars indicate different stream segments. Dredging of the irrigation ditch occurred between May 1988 and October 1989. The upper zone sampled was above the point of the irrigation diversion. The ditched segment existed prior to dredging in 1988 but had become overgrown nearly to the point of obstructing any flow. After dredging, it received most of the discharge from the system. The channel received nearly all the flow from the springs in area 4 during the 1988 sample, but only 20% or less of the total flow in subsequent samples.

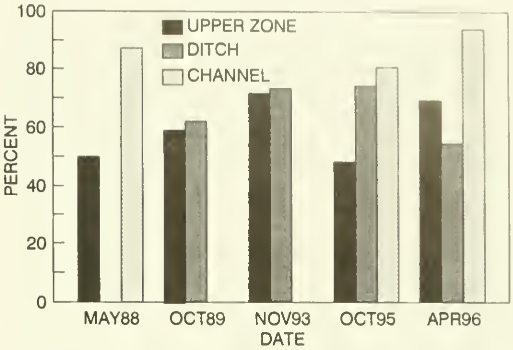

Fig. 4. Percent traps with non-zero catch, area 4, from May 1988 through April 1996. Bars indicate different stream segments. Dredging of the irrigation ditch occurred between May 1988 and October 1989. The channel received nearly all the flow from the springs in area 4 during the 1988 sample, but only 20% or less of the total flow in subsequent samples.

never more than 75% of the traps caught fish. The old channel zone continues (in both 1995 and 1996) to have a larger percentage of traps catching fish than either of the other 2 zones (Fig. 3).

Catch per trap hour may also be used to estimate relative fish populations. The 3 highest average catch rates were observed in the channel below the present point of diversion, and the highest value of any was observed in 1988, prior to the dredging (Fig. 4). Although catch values were still highest in 1995 and 1996 in the old channel zone, they have not returned to levels observed in 1988. Catches from the upstream and ditched zones have varied much less during the sample period.

These data indicate that the natural channel was the most productive site for desert dace prior to the ditch dredging, and that it still provides habitat which is superior to the ditch, even 8 yr after the dredging and with <20% of the total discharge.

The observed aggregation of fish above the diversion (evident in the cumulative catch data since 1993) bears examination. If habitat in the ditch is unsuitable, desert dace may avoid the ditched zone and accumulate in the upstream zone. Because no aggregation of fish in this zone was observed in 1988 or 1989, it seems likely to be the result of a behavioral response to the changed conditions.

The higher mean water velocities observed in the ditch (24.9 cm/s) relative to the upstream zone (17.3 cm/s) suggest that desert dace may avoid higher velocity flows. It is likely that smaller fish avoid higher velocity flows in the ditched section and accumulate in the region immediately upstream from it. Although this explanation does not account for the relatively low abundance of fish in the old channel, other factors, including reproductive success and differences in habitat quality, may be important. The absence of the aggregation upstream from the ditch in 1988 may reflect a general population reduction resulting from the ditching.

Distribution of desert dace reflects potentially interacting factors including temperature, dissolved oxygen concentration, and current velocity. Distribution may also be affected by interactions with other species, particularly speckled dace. Studies are necessary to identify and assess the mechanisms of such interactions. An additional area of interest would be to assess the relative degree of isolation of the 7 population units identified in this study to determine whether there are any behavioral, ecological, or genetic differences among these groups.

CONCLUSIONS

In recent years desert dace have been subjected to relatively minor disturbance compared with many other native fish species in the Great Basin. Most of the sites historically occupied by desert dace retain suitable habitat, though it has generally been modified to some extent. Disturbance levels may have been higher at times in the 1960s (Nyquist 1963). Desert dace populations in Soldier Meadow have been relatively stable since 1989, but most desert dace habitats have been substantially altered over the years, and we cannot now directly assess the magnitude of any persistent population reductions that may have occurred before that time. Desert dace populations persist in the modified thermal waters that now characterize Soldier Meadow; however, the data from area 4 demonstrate that adverse effects of habitat modifications linger for many years.

It is appropriate to consider management options for this unique fish. Their preservation requires continued physical protection of springs and flowing waters in Soldier Meadow from excessive grazing and prohibition of the introduction of nonnative organisms. Restoring the water to natural stream channels should also be incorporated into any management plan because of the potential positive impacts from improving habitat quality. Consequences of such water management for the endemic springsnails should either be neutral or positive. They are generally abundant in the springs where they occur, and losses from restoration of flows should be offset by increased habitat stability.

Desert dace seem relatively secure under current conditions. However, the small number of occupied sites, restricted geographical distribution, and generally unknown but possibly specialized habitat requirements of the fish argue strongly for continued monitoring and increased investigation into factors regulating populations. Growing demands on aquatic resources of the Great Basin make it clear that increased awareness of and protection for this unique fish will be necessary for their long-term survival.

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HELMINTHS OF THE SOUTHWESTERN TOAD, *BUFO MICROSCAPHUS*, WOODHOUSE'S TOAD, *BUFO WOODHOUSII* (BUFONIDAE), AND THEIR HYBRIDS FROM CENTRAL ARIZONA

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ABSTRACT.—The gastrointestinal tracts, lungs, and urinary bladders from 77 *Bufo microscaphus*, 61 *Bufo woodhousii*, and 8 of their hybrids were examined for helminths. One species of trematode (*Glypthelmins quieta*), 1 species of cestode (*Distoichometra bufonis*), and 5 species of nematodes (*Aplectana incerta, A. itzocanensis, Rhabdias americanus, Physaloptera* sp., and *Physocephalus* sp.) were found. The greatest prevalence (41%) and mean intensity (231.7) were recorded for *Aplectana incerta* in *Bufo woodhousii*. It appears hybrids harbor fewer parasites than either parent species.

Key words: helminths, Bufo microscaphus, Bufo woodhousii, *hybrids, Arizona.*

The southwestern toad (*Bufo microscaphus* Cope, 1866) is presently recognized as 3 allopatric subspecies: *B. m. californicus* Camp, 1915, which occurs in coastal southern California and northwest Baja California; *B. m. microscaphus* Cope, 1866, found in southern Nevada and Utah, Arizona, and New Mexico; and *B. m. mexicanus* Brocchi, 1879, which occurs in the Sierra Madre Occidental of central México south to Durango (Price and Sullivan 1988). Woodhouse's toad (*Bufo woodhousii* Girard, 1854) is recognized as 4 subspecies: *B. w. woodhousii* Girard, 1854 occurs in eastern Montana and North Dakota, south through the plains states to central Texas and west of the Rocky Mountains from Idaho south to Colorado and Arizona with isolated populations in west Texas, southeastern California, and along the Oregon-Washington border; *Bufo w. australis* Shannon and Lowe, 1955 is found from central Colorado through New Mexico and Arizona to Sonora, México, and along the Rio Grande drainage into southwest Texas and adjacent México; *Bufo w. velatus* Bragg and Sanders, 1951 is restricted to northeast Texas; and *B. w. fowleri* Hinckley, 1882 is widespread throughout much of the eastern United States south to the Gulf Coast and west to eastern Texas (Behler and King 1979). The toads examined during this study, *B. m. microscaphus* and *B. w. australis*, are known to hybridize in Arizona (Sullivan 1986, Sullivan and Lamb 1988).

Although there are reports of helminths from *B. microscaphus* (Parry and Grundmann 1965) and *B. woodhousii* (Trowbridge and Hefley 1933, Brandt 1936, Walton 1938, Reiber et al. 1940, Kuntz 1941, Kuntz and Self 1944, Rankin 1945, Fantham and Porter 1948, Frandsen and Grundmann 1960, Parry and Grundmann 1965, Campbell 1968, Brooks 1976, Jilek and Wolff 1978, Baker 1985, Hardin and Janovy 1988, McAllister et al. 1989), populations of these toads from Arizona have not been examined. Concern over declining amphibian populations (Heyer et al. 1994) has increased interest in the possible negative effects of parasites on toads. The purpose of this paper is to report on helminths of these toads and their hybrids from Arizona.

This investigation of parasitism in these toads addresses a hypothesis of hybrid zone theory and species boundaries. The hypothesis that populations of hybrid individuals with reduced fitness act as barriers to gene flow between 2 species separated by a hybrid zone (Barton 1979, 1980) could have several mechanisms. One mechanism, increased parasitism of hybrids, is evaluated in this study. Two previous studies of parasitism in vertebrates are split. Hybrid mice (*Mus musculus* × *Mus domesticus*), specifically backcrossed hybrids, had greater numbers of cestode and nematode parasites than either parental species (Sage et al. 1986). Prevalence of monogenean parasites for hybrid minnows (*Barbus barbus* × *Barbus meridionalis*) was

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positively associated with the percentage of *B. meridionalis* genes (Le Brun et al. 1992). If we find that hybrid toads have greater parasitism than each toad species, then parasitism may be a mechanism that reduces hybrid fitness and contributes to the barrier between these 2 toad species.

MATERIALS AND METHODS

One hundred forty-six toads were collected in Arizona during 1991–1995; snout-vent length (SVL) was measured to the nearest mm after a minimum of 6 mon in 70% ethanol storage. Toads were identified using a hybrid index (HI) and advertisement call structure, if available. Following Blair (1955), Sullivan (1986), and Sullivan and Lamb (1988), we evaluated the degree of expression of 4 characters to generate the HI score for each toad: dark ventral pigmentation, cranial crest, dorsal stripe, and pale coloration across the eyelids. A numerical score (0, 1, 2, 3) was assigned for each of the following 4 character states: present, weakly present, very weakly present, or absent. A score of 3 was assigned for the presence of dark ventral pigmentation, cranial crests, a dorsal stripe, and absence of a pale bar across the eyelids. This yields scores near 12 (4 × 3) for *B. woodhousii* and 0 (4 × 0) for *B. microscaphus.* Numerous other studies of hybridization between toad species have used a morphological hybrid index such as this (Volpe 1959, Meacham 1962, Henrich 1968, Zweifel 1968). All toads from sites of sympatry with scores of 4 through 8 were considered hybrids, as were all toads with intermediate advertisement calls. Intermediate calls are typical of hybrid toads between these species (Sullivan 1995), and calls have long been used to delimit hybrid toads of other species pairs (Blair 1956, Zweifel 1968, Green 1982). Seventy-seven *Bufo microscaphus* (mean SVL = 61.4 mm ± 8.7 *s*, range 34–86 mm, 67 males, 10 females); 61 *Bufo woodhousii* (mean SVL = 74.5 mm ± 8.8 *s*, range 49–91 mm, 53 males, 8 females), and 8 hybrids (mean SVL = 60.5 mm ± 8.4 *s*, range 45–72 mm, 7 males, 1 female) were examined. Kruskal-Wallis test statistic (45.92, 2 df, $P < 0.001$) indicates significant difference in SVLs for the samples examined. After examination all specimens were deposited in the herpetology collection of Arizona State University (ASU), Tempe. Collection localities and ASU accession numbers are given in Appendix 1.

Toads were anesthetized by immersion in 1 g/l solution of tricaine methane sulfonate (MS-222, Sigma, St. Louis, MO). Heart, liver, thigh muscle, and kidney were removed and frozen for future genetic analyses. Toads were then fixed in neutral-buffered 10% formalin and moved to ethanol for storage following procedure outlined by Simmons (1987). The body cavity was opened by a longitudinal incision from vent to throat, and the gastrointestinal tract was removed by cutting across the esophagus and rectum. The esophagus, stomach, small intestine, large intestine, lungs, bladder, and coelom were examined under a dissecting microscope. No helminths were found in the esophagus or urinary bladder. All helminths were removed and identified using a glycerol wet mount. Specimens were placed in vials of alcohol and deposited in the U.S. National Parasite Collection, Beltsville, Maryland 20705: (accession numbers, Appendix 1).

RESULTS AND DISCUSSION

Prevalence, site, and mean intensity for each parasite are given in Table 1. Terminology is in accordance with Margolis et al. (1982). One species of trematode (*Glypthelmins quieta* [Stafford, 1900]), 1 species of cestode (*Distoichometra bufonis* Dickey, 1921), and 5 species of nematodes (*Aplectana incerta* Caballero, 1949, *Aplectana itzocanensis* Bravo Hollis, 1943, *Rhabdias americanus* Baker, 1978, *Physaloptera* sp. [larvae only], and *Physocephalus* sp. [larvae only]) were found. It would appear from Table 1 that both species and their hybrids are susceptible to infection by the same parasites. The greatest prevalence (41%) and mean intensity (231.7) in our study were recorded for *Aplectana incerta* in *Bufo woodhousii.* Thirty-four of 77 (44%) *Bufo microscaphus* (30/67, 45% males; 4/10, 40% females), 51 of 61 (84%) *B. woodhousii* (45/53, 85% males; 6/8, 75% females), and 4 of 8 (50%) hybrids (3/7 males, 1/1 female) were infected. Males and females of both *Bufo microscaphus* ($\chi^2 = 1.17$, 1 df, $P > 0.05$) and *B. woodhousii* ($\chi^2 = 2.79$, 1 df, $P > 0.05$) did not differ significantly in helminth prevalence. There were too few female hybrid toads for chi-square analysis. There was statistical difference in abundance of nematodes between *B. microscaphus* and *B. woodhousii* ($\chi^2 = 23.72$,

TABLE 1. Prevalence, mean intensity (range), and location of helminths from *Bufo microscaphus*, *B. woodhousii*, and their hybrids from Arizona.

	Bufo microscaphus ($N = 77$)			*Bufo woodhousii* ($N = 61$)			Hybrids ($N = 8$)		
Parasite species	Prevalence (%)	Intensity (range)	Location	Prevalence (%)	Intensity (range)	Location	Prevalence (%)	Intensity (range)	Location
TREMATODA									
Glypthelmins quieta	1	1.0	b	2	2.0	b	13	1.0	b
CESTODA									
Distoichometra bufonis	14	2.9 (1-6)	b	38	2.0 (1-8)	b	13	1.0	b
NEMATODA									
Aplectana incerta	1	156.0	b,c	41	231.7 (23-564)	b,c	—		
Aplectana itzocanensis	19	75.0 (1-373)	b,c	26	43.2 (1-204)	b,c	25	1.0	c
Physaloptera sp. (larva)	16	5.5 (1-31)	a	5	6.0 (2-11)	a	13	1.0	a
Physocephalus sp. (larvae)	1	104.0	d	—			—		
Rhabdias americanus	5	2.0 (1-3)	e	38	21.7 (1-111)	e	—		

a = stomach, b = small intestines, c = large intestines, d = cysts on stomach wall, e = lungs.

1 df, $P < 0.001$). When the intermediate prevalence (50%) of the small hybrid sample ($N = 8$) was included in the chi-square calculation, statistical significant difference remained ($\chi^2 = 23.97$, 2 df, $P < 0.001$).

To test for difference in infection rate, we used a Kruskal-Wallis rank-order statistic because of the great variation in mean intensity of parasites harbored by *B. microscaphus*, *B. woodhousii*, and their hybrids (116.3, 19.4, 1.3, respectively) and the relatively small sample of hybrids ($N = 8$). This test revealed that hybrid individuals had fewer parasites than do individuals of either species. Examination of more hybrids could strengthen this result. Subsequent work to determine the importance of age, genetic factors, nutrition, and ecology would also help to establish the significance of hybrid ancestry on parasite levels.

Infected frogs appeared healthy; i.e., none were emaciated and there were no gross abnormalities. Thus, the presence of helminths did not appear to adversely affect the populations of *B. microscaphus*, *B. woodhousii*, or their hybrids. In a study on Couch's spadefoot (*Scaphiopus couchii*) from Arizona, Tinsley (1990) found no correlation between presence of the trematode *Pseudodiplorchis americanus* and mating success, although the presence of *P. americanus* reduced fat reserves during hibernation.

Bufo microscaphus is a new host record for *Distoichometra bufonis*, *Aplectana incerta*, *A. itzocanensis*, *Physocephalus* sp., and *Rhabdias americanus*. *Bufo woodhousii* is a new host record for *Aplectana incerta* and *Physaloptera* sp. *Bufo w. woodhousii* has been reported by Baker (1985) to host *Aplectana itzocanensis*. *Bufo microscaphus* × *B. woodhousii* hybrid is a new host record for *Distoichometra bufonis*, *Glypthelmins quieta*, *Aplectana itzocanensis*, and *Physaloptera* sp. *Glypthelmins quieta* in Arizona is a new locality record.

With the exception of *Glypthelmins quieta*, all helminths found in our study have been previously reported in other desert toads from Arizona (Table 2). *Glypthelmins quieta* has previously been reported in *Bufo microscaphus* from Utah (Parry and Grundmann 1965) and in *Bufo woodhousii* from Nebraska (Brooks 1976). It is widely distributed in anurans in North America (Prudhoe and Bray 1982). The distribution of *Distoichometra bufonis*, *Aplectana incerta*, *A. itzocanensis*, *Physaloptera* sp., and *Rhabdias americanus* in North American toads has previously been discussed (Goldberg and Bursey 1991a, Goldberg et al. 1996). *Aplectana incerta*, *A. itzocanensis*, and *Rhabdias americanus* have direct life cycles; *Distoichometra bufonis*, *Physaloptera* sp., and *Physocephalus* sp. have indirect life cycles and require at least 1 intermediate host (Anderson 1992, Smyth 1994). Because these helminths are not species specific and occur in a variety of amphibians, the distribution of intermediate hosts may play an important role in determining the distribution of those parasites with indirect life cycles. The conditions responsible for determining distribution of the parasites with direct life cycles have yet to be defined.

TABLE 2. Helminth community of desert toads from Arizona.

Helminth	Host	Reference
TREMATODA		
Glypthelmins quieta	*Bufo microscaphus*	This study
	B. woodhousii	This study
Pseudodiplorchis americanus	*Scaphiopus couchii*	Tinsley 1990
CESTODA		
Distoichometra bufonis	*Bufo cognatus*	Goldberg and Bursey 1991a
	B. microscaphus	This study
	B. punctatus	Goldberg and Bursey 1991b
	B. retiformis	Goldberg et al. 1996
	B. woodhousii	This study
	Scaphiopus couchii	Goldberg and Bursey 1991a
Nematotaenia dispar	*Bufo alvarius*	Goldberg and Bursey 1991a
NEMATODA		
Aplectana incerta	*Bufo microscaphus*	This study
	B. retiformis	Goldberg et al. 1996
	B. woodhousii	This study
	Scaphiopus couchii	Goldberg and Bursey 1991a
Aplectana itzocanensis	*Bufo alvarius*	Goldberg and Bursey 1991a
	B. cognatus	Goldberg and Bursey 1991a
	B. microscaphus	This study
	B. punctatus	Goldberg and Bursey 1991b
	B. retiformis	Goldberg et al. 1996
	B. woodhousii	This study
Oswaldocruzia pipiens	*Bufo alvarius*	Goldberg and Bursey 1991a
	B. cognatus	Goldberg and Bursey 1991a
	B. punctatus	Goldberg and Bursey 1991b
	B. retiformis	Goldberg et al. 1996
	Scaphiopus couchii	Goldberg and Bursey 1991a
Physaloptera sp. (larva)	*Bufo alvarius*	Goldberg and Bursey 1991a
	B. cognatus	Goldberg and Bursey 1991a
	B. microscaphus	This study
	B. retiformis	Goldberg et al. 1996
	B. woodhousii	This study
Physocephalus sp. (larva)	*Bufo alvarius*	Goldberg and Bursey 1991a
	B. microscaphus	This study
	B. retiformis	Goldberg et al. 1996
Rhabdias americanus	*Bufo alvarius*	Goldberg and Bursey 1991a
	B. cognatus	Goldberg and Bursey 1991a
	B. microscaphus	This study
	B. retiformis	Goldberg et al. 1996
	B. woodhousii	This study

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APPENDIX 1

Localities and museum (ASU) numbers for specimens examined:

Bufo microscaphus: Maricopa County (*N* = 6) (34°00′N, 112°45′W, elev 603 m) ASU 30360-61, 30369-72; Yavapai County (*N* = 61); 7 from (34°24′N, 112°13′W, elev. 1323 m) ASU 30328-31, 30347-49; 6 from (34°06′N, 112°09′W, elev 603 m) (ASU 29166-67, 29170-71, 30351, 30375); 4 from (34°04′N, 112°09′W, elev 488 m) (ASU 30377, 30379-81); 34 from (34°05′N, 112°07′W, elev 616 m) ASU 28845-50; 28852-57, 29172-83, 30334-40; 30386-88; 10 from (34°24′N, 112°08′W, elev. 1140 m) ASU 30487-96; Coconino County (*N* = 10) (34°24′N, 112°08′W, elev 2094 m) ASU 30477-86.

Bufo woodhousii: Maricopa County (*N* = 53); 14 from (33°38′N, 112°28′W, elev 410 m) ASU 28821-27, 28829-31, 30356-59; 19 from (33°56′N, 112°08′W, elev 628 m) ASU 28818-19, 28828, 28835, 30362-64, 30366-68, 29151-59; 2 from (33°36′N, 112°15′W, elev. 365 m) ASU 28834, 28836; 7 from (33°39′N, 112°14′W, elev. 389 m) ASU 30497-503; 11 from (33°36′N, 112°11′W, elev. 372 m) ASU 30504-14; Yavapai County (*N* = 8); 7 from (34°06′N, 112°09′W, elev 488 m) (ASU 29165, 29167-69; 30345, 30350, 30355, 30376); 1 from (34°04′N, 112°09′W, elev 488 m) (ASU 30385).

Hybrids: Yavapai County (*N* = 8); 7 from (34°06′N, 112°09′W, elev 603 m) ASU 30346, 30352-54, 30373-74, 30382; 1 from (34°04′N, 112°09′W, elev 488 m) ASU 30378.

Accession numbers for helminths in the U.S. National Parasite Collection (USNPC):

Bufo microscaphus: *Distoichometra bufonis* (85910); *Glypthelmins quieta* (85921); *Aplectana incerta* (85911); *Aplectana itzocanensis* (85912); Physalopteridae (85915); *Physocephalus* sp. (85914); *Rhabdias americanus* (85913). ***Bufo woodhousii:*** *Distoichometra bufonis* (85916); *Glypthelmins quieta* (85921); *Aplectana incerta* (85917); *Aplectana itzocanensis* (85918); Physalopteridae (85920); *Rhabdias americanus* (85919). **Hybrids:** *Distoichometra bufonis* (85922); *Glypthelmins quieta* (85921); *Aplectana itzocanensis* (85923); Physalopteridae (85924).

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JUVENILE RAZORBACK SUCKER (*XYRAUCHEN TEXANUS*) IN A MANAGED WETLAND ADJACENT TO THE GREEN RIVER

Timothy Modde[1]

Key words: razorback sucker, floodplain, wetland, juvenile.

The razorback sucker (*Xyrauchen texanus*) is a large, endemic catostomid of the Colorado River drainage. It was once widespread and abundant throughout the basin (Minckley et al. 1991). Species abundance and distribution declined following construction of mainstem dams and the introduction of many nonnative fishes (Behnke and Benson 1983, Carlson and Muth 1989). The razorback sucker was federally listed as endangered in 1991 (USFWS 1991).

The largest riverine population of razorback sucker is in the middle Green River (Lanigan and Tyus 1989). These fish spawn successfully (Tyus and Karp 1990), but Lanigan and Tyus (1989) reported little or no recruitment. Razorback sucker larvae in the Green River drift downstream from spawning sites (Robert Muth, Larval Fish Laboratory, Colorado State University, Fort Collins, CO), but few juvenile have been found and little is known of their habitat needs. Taba et al. (1965) captured 8 juveniles (90–115 mm total length [TL]) from Colorado River backwater habitat in surveys from 1962 to 1964 between Moab and Dead Horse Point, Utah. More recently, Gutermuth et al. (1994) collected 2 juveniles (37 mm and 39 mm) from a lower Green River backwater in 1991 and 2 others (59 mm and 29 mm) in a backwater on the Ouray National Wildlife Refuge in 1993 (Robert Muth, Larval Fish Laboratory, Colorado State University, personal communication). This note reports occurrence of juvenile and adult razorback suckers in a wetland adjacent to the Green River in Utah.

Old Charley Wash is a 60-ha wetland on the Ouray National Wildlife Refuge in Uintah County, northwest Utah, adjacent to river kilometer (RK) 402 on the Green River. The wash is a historical type IV wetland (Cowardin et al. 1979) with smartweed (*Polygonum sp.*) and sago pond weed (*Potamogeton pectinatus*) being the primary aquatic plants. The natural levees of the wetland have been reinforced with dikes to retain water through the summer and fall periods. Water in- and outflow is controlled at flows <481 m^3/s. Water enters the inlet at river flows of approximately 240 m^3/s. Typical management is to fill in spring and then maintain water through the summer and autumn.

The outlet structure at Old Charley Wash was modified in April 1995 to facilitate fish capture by creating a drainable, 12-m concrete-lined channel in which fish could be concentrated and captured with seines.

Spring flow of the Green River peaked at about 595 m^3/s in 1995 and inundated Old Charley Wash between 23 May and 1 July. Inundation was at flows >481 m^3/s. The wash was dry prior to inundation. Maximum depth of the wetland was >2 m. Fish in the wetland were isolated from the river; when runoff subsided, no additional water was added. Fishes were sampled by fyke and trammel nets, minnow and light traps, and seines. Collections were weekly from 23 May to 1 July and every 2 wk from 2 July to 31 August. The wetland was drained from 25 September to 12 October, and fishes were collected from the outlet every other day during the first 2 wk and daily (except 9 October) during the 3rd week. Twenty-eight juvenile razorback sucker were collected when Old Charley Wash was drained in the fall of 1995 ($\bar{x}$ = 94 mm TL [range = 74–125 mm] and 9.5 g [range = 3–18 g]; voucher specimens, catalog number LFL 24874, Larval Fish Laboratory, Colorado State University). Eight (461–525 mm TL; 1034–1650 g) adults also were captured, 6 prior to and 2 during the draining process. A total of 10.1 metric tons of fish were collected during draining. The following species were represented in order of contribution by weight: *Cyprinus carpio*, *Pimephales promelas*, *Lepomis cyanellus*, *Ictalurus punctatus*, *Ameiurus melas*, *Cyprinella lutrensis*, *Pomoxis nigromaculatus*, *Xyrauchen texanus*, *Esox lucius*, *Gila atraria*, *Catostomus latipinnis*, *Catostomus commersoni*, *Ptychocheilus lucius* (7 individuals ranging in TL between 175 and 207 mm, and weight from 33 to 62 g), *Gila robusta*, and *Culaea inconstans*.

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Tyus and Karp (1990) reported that razorback sucker spawn on the ascending limb of the hydrograph, allowing drifting larvae to disperse during peak runoff and thus maximizing access to wetland habitats. It is unknown whether the juveniles collected during draining originated from riverine spawning sites or were produced in Old Charley Wash. However, their occurrence in Old Charley Wash in 1995 supports speculation (Tyus and Karp 1990, Modde et al. 1966) that floodplains may be important razorback sucker nursery areas.

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CONFIRMATION OF COSEXUALITY IN PACIFIC YEW (*TAXUS BREVIFOLIA* NUTT.)

K. E. Hogg[1], A. K. Mitchell[1,2], and M. R. Clayton[1]

Key words: Pacific yew, Taxus brevifolia, *dioecious, cosexuality, British Columbia, pollen, seed.*

Unlike most evergreen conifers in our forests, which have both pollen and seed on a single tree, Pacific yew (*Taxus brevifolia* Nutt.) is dioecious, the 2 sexes being segregated on different trees (Rudolf 1974, Taylor and Taylor 1981, Bolsinger and Jaramillo 1990, Hils 1993).

In July 1993 branch samples of *T. brevifolia* were taken from an undisturbed stand of coastal Douglas-fir (*Pseudotsuga menziesii*) on southern Vancouver Island (48°26′N. lat.; 123°28′W. long.) near Victoria, British Columbia. One of the samples was observed to have both male and female reproductive structures (bud scales partially removed) on a single twig (Fig. 1).

Occasionally, male and female structures can occur on the same tree (Taylor and Taylor 1981). In the instances reported (Owens and Simpson 1986, DiFazio 1995), female and male structures occurred together only on branches of predominantly male trees. We observed this phenomenon, termed cosexuality (Lloyd 1980), on a single yew tree. On one branch, female and male reproductive structures were observed within a few mm of each other (Fig. 1) on an otherwise male tree. The structures were visually identical to respective buds from other dioecious trees. In a study by DiFazio (1995), cosexuality was found in 17 of 58 male trees (29.3%). It is not known whether these female buds found on male trees produce viable seed.

Reproductive buds of the Pacific yew can be visually differentiated throughout the year (Taylor and Taylor 1981) and are usually located on the underside of the shoot on noncurrent growth. Male buds are small (2–3 mm), round, and green, and they generally occur in clusters (Fig. 2). They consist of a number of distinct segments made up of pillowlike structures (microsporangia) in which the pollen mature. In spring microsporangia burst the bud scales (Fig. 3) and pollen is released. Female buds generally occur singly (Fig. 4) and are erect, oval (2–3 mm), and green. The female bud matures slowly through spring and summer with the ovule (Fig. 5) growing through the bud scales and revealing the micropyle (opening for pollen). Beginning in late July or early August, depending on location, a fleshy red aril (berry) around the hard-coated seed becomes visible.

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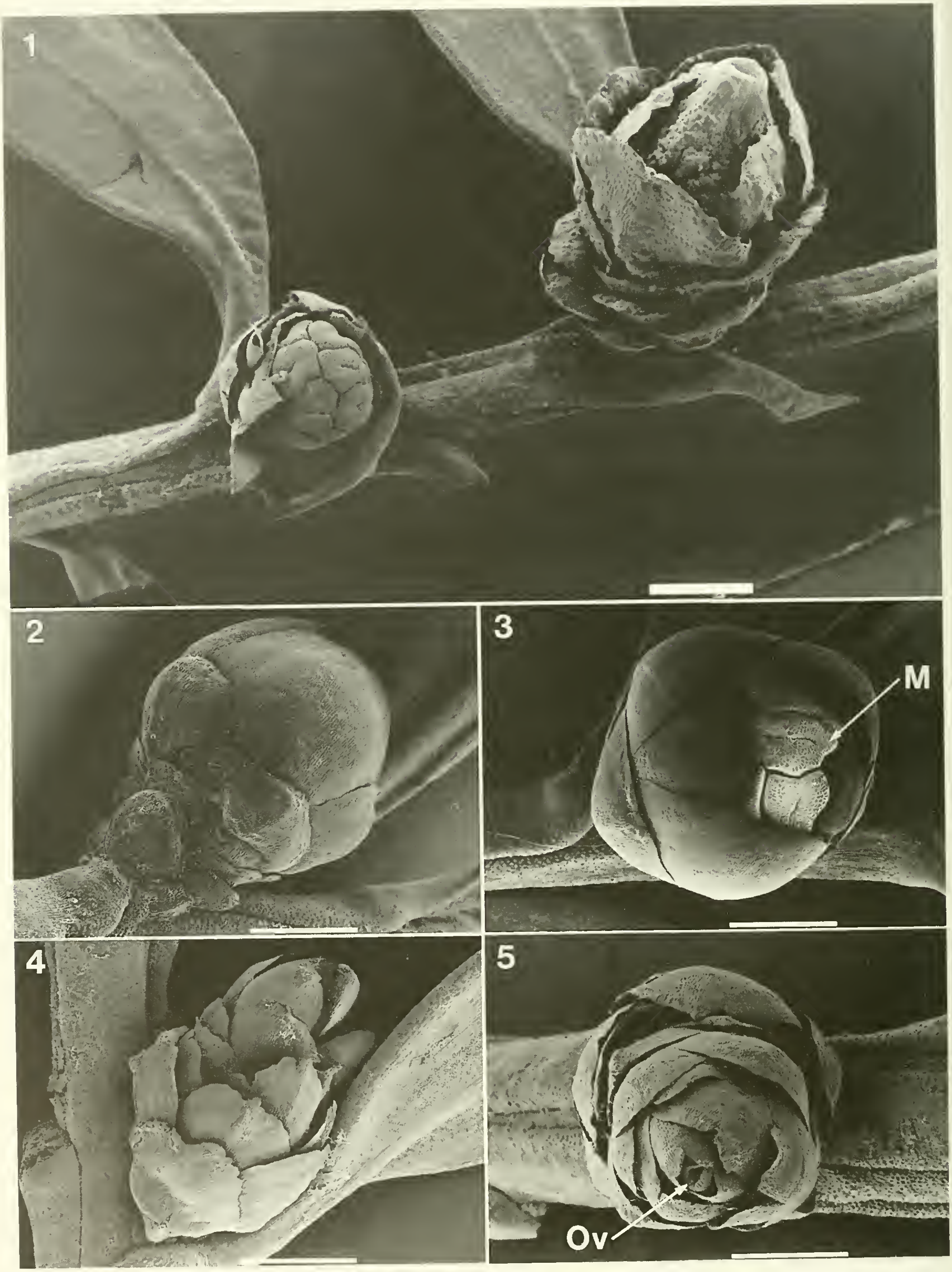

Figs. 1–5. Scanning electron micrograph confirming cosexuality in Pacific yew (*Taxus brevifolia*) from southern Vancouver Island, British Columbia. Scale bar = 1 mm in each figure. 1, Male bud (left) and female bud (right), both with bud scales partially removed, on the same twig. 2, Young male bud (March) prior to shedding of pollen; bud scales intact. 3, Young male bud (March) showing the emerging microsporangia (M); bud scales intact. 4, Young female bud (March); bud scales intact. 5, Mature female bud (August) showing the ovule tip (Ov) and micropyle emerging through the center of the intact bud scales.

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DIURNAL ABOVEGROUND ACTIVITY BY THE FOSSORIAL SILVERY LEGLESS LIZARD, *ANNIELLA PULCHRA*

David J. Germano[1] and David J. Morafka[2]

Key words: activity, lizards, Anniella, *California, reptiles, behavior.*

Anniella pulchra is a limbless, fossorial lizard. This species occurs from Antioch, California, to northern Baja California, and is often found on dune formations and in sandy habitats where it typically can be captured by raking the soil under bushes (Miller 1944). It can also be found in several low, coastal mountain ranges (Stebbins 1985), and its range extends into the San Joaquin Valley and to the edge of the Sonoran Desert in eastern San Diego County (Klauber 1932, Jennings and Hayes 1994). It seems to prefer moist soils (Miller 1944) where it is able to drink (Fusari 1985). Because of its fossorial habit, *A. pulchra* is rarely found moving aboveground, but it sometimes can be found on the surface at dusk or in the evening (Stebbins 1985). Here we report the previously unrecorded finding of a single *A. pulchra* moving aboveground during the middle of the day.

On 27 April 1995 we were driving on Crocker Springs Road heading northeast over the southern end of the Temblor Mountains. This road is unpaved over the Temblors, and we found 1 *A. pulchra* on a hard-packed section of the road. The location was at 769 m (2500 ft) in San Luis Obispo County, approximately 1.5 km west of the county boundary with Kern County. The lizard, an adult male 140 mm snout-vent length (217 mm total length), was found at approximately 1425 h.

The day was partly cloudy and the air temperature when the lizard was found was about 24°C. Although the road is not steeply inclined at the location, the surrounding topography traversed by this section of the road is a steep hillside of about a 45-degree slope. Dominant vegetation on the hillside is alkali goldenbush (*Haplopappus acradenius*), and no sandy soil occurs near the location where we found the lizard. The lizard was stretched out on the road, which it probably was crossing when we saw it. Unfortunately, we ran over the lizard with our vehicle and were not able to watch its movement after we found it. We salvaged the body and deposited it in the museum of the California Academy of Science (specimen #CAS201173, taken under California Department of Fish and Game permit #1111). Besides the injuries we inflicted on the specimen, there were no other signs of injury or obvious infestations by parasites. This is the first observation we know of showing that *A. pulchra* sometimes makes aboveground movements during the day.

Midday aboveground activity of *A. pulchra* appears to be a rare behavior. It is possible that this lizard has narrow physiological tolerances that often prevent surface activity, particularly in full sun. *A. pulchra* has a lower preferred body temperature than most other lizards (Bury and Balgooyen 1976), and its requirement for moist soil and free water has been known for almost a century (Coe and Kunkel 1907). We found this lizard active at an air temperature of about 24°C, which is consistent with its preferred thermal range of 24–25°C (Bury and Balgooyen 1976). Limited surface activity, especially away from plant cover, may also be due to predator avoidance. Because limbless lizards are adapted for burrowing, their ability to move quickly aboveground is limited (Gans 1975). These physiological and behavioral constraints likely limit the aboveground activity of *A. pulchra* to short durations and distances.

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